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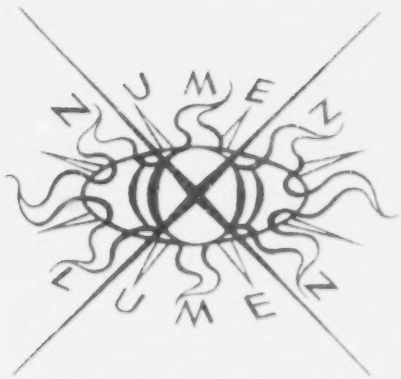

DISTRIBUTIONAL ECOLOGY AND BEHAVIORAL THERMOREGULATION OF FISHES IN RELATION TO HEATED EFFLUENT FROM A STEAM-ELECTRIC POWER PLANT (LAKE MONONA, WISCONSIN)

by

William H. Neill
John J. Magnuson

1972

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Neill, W. H., and Magnuson, J. J.

Wisconsin University, Madison, Department of Zoology, ~~and Water Resources Center.~~

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Cooling water for a 220-megawatt power plant is pumped from 5 m beneath Lake Monona's surface, heated about 10 C, and discharged into the littoral zone. Maximum temperatures in the effluent-outfall area approach 35 C in summer, and 14 C in winter; unheated parts of the littoral zone rarely exceed 29 C.

To assess the distributional responses of fish to the operation of the power plant, the outfall area and two reference areas were electro-fished thirty times over a one-year period. Some fishes found in the reference areas avoided the outfall area, whereas other fishes were at higher concentration in the outfall area relative to the reference sites. The tendency for a species-size class to concentrate in or avoid the outfall area generally did not reverse from season to season or from day to night. Size-dependent movements of the fish tended to obscure the difference in growth rate of young fishes between study areas.

Integrated laboratory studies on six species and field results suggest that fishes were distributed within the outfall area according to their different temperature preferenda. Also, thermoregulatory behavior was overridden by feeding behavior even though zooplankton food was more abundant in the outfall area. ~~(Neill-Wisconsin).~~

*Electric powerplants, *Outlets, *Lake, *Seasonal, *Fish, Temperature, Zooplankton growth rates, Wisconsin,

*Feeding behavior, *Fish food, ~~*Field, *Laboratory,~~ *Temperature preference, Lake Mendota, Dane County, Wisconsin, *Perca flavescens*, *Cottus bairdi*, *Morone mississippiensis*, *Ictalurus melas*, *Lepisosteus osseus*, *Cyprinus carpio*.

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William H. Neill

Wisconsin University-Madison.

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William H. Neill
John J. Magnuson

Department of Zoology
College of Letters and Science
The University of Wisconsin-Madison

March 1972

Partial Technical Completion Report

Project Number OWRR B-028-WIS

Principal Investigators

John J. Magnuson, Professor, Department of Zoology
William H. Neill, Research Assistant, Department of Zoology

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Water Resources Center
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March 1972

Abstract

Cooling water for a 220-megawatt power plant is pumped from 5 m beneath Lake Monona's surface, heated about 10 C, and discharged into the littoral zone. Maximum temperatures in the effleunt-outfall area approach 35 C in summer and 14 C in winter; unheated parts of the littoral zone rarely exceed 29 C.

To assess distributional responses of fishes to operation of the power plant, the outfall area and two reference areas were electro-fished on 30 dates between 8 August 1968 and 21 August 1969. Some fishes avoided the outfall area; these were yellow perch, mottled sculpin, subadult yellow bass, and subadult black bullhead. Others were occasionally or usually concentrated in the outfall area relative to reference areas--longnose gar, adult carp, adult yellow bass, young pumpkinseed, bluegill, and largemouth bass. The tendency for a species-size class to concentrate in or avoid the outfall area generally did not reverse from season to season or from day to night.

Any differences in growth rate of young fishes among outfall and reference areas were obscured by size-dependent movements of the fish.

In August 1970, body temperature of fishes in the outfall area varied with species and time of day. During afternoon, median temperatures of carp, pumpkinseed, bluegill, and largemouth bass were higher than 29 C, while those of yellow bass, rock bass, black crappies and yellow perch were lower than 29 C. At night, only longnose gar and carp had median body temperatures higher than 29 C.

Young bluegill collected during summer 1970 from the outfall area had estimated acclimation temperatures between 29.4 and 31.3 C, even though temperatures between 25 and 36 C were available. To have had acclimations between 29.4 and 31.3 C, the fish must have avoided exposure to temperatures higher than about 31.5 C. This conclusion agreed substantially with the distribution of body temperatures of young bluegill; the highest body temperature among 31 specimens was 31.8 C.

Temperatures at which fishes lived in the outfall area during summer 1970 were positively correlated ($p < 0.01$) with the degree to which they were concentrated in the outfall area during the two previous summers. The strength of the correlation, involving data from ten species, argued that, during summer, temperature was the primary factor governing not only distribution of fishes within the outfall area but also the abundances of fishes in the outfall area relative to unheated parts of the littoral zone.

Moreover, integration of field and laboratory results suggested that fishes were distributed within the outfall area according to their different temperature preferenda. Preferred temperatures of six Lake Monona fishes were measured by allowing each of several specimens to behaviorally regulate the temperature of its tank. Midpoint of the preferred temperature range agreed well with the median body temperature recorded in the outfall area during afternoon (considering, in the case of yellow perch, that temperatures below 26.5 C were not available in the outfall area): carp, 31.8 C (laboratory), 30.6 C (field); bluegill, 30.3, 29.4; largemouth bass, 29.1, 29.7; black crappie, 28.3, 28.3; rock bass, 27.3, 27.5; and yellow perch, 23.4, 27.1.

In other laboratory experiments, bluegill and yellow perch were required to partition time between an environment with preferred temperature and an environment with food but either warmer or cooler than the preferred temperature. Each species made forays for food into water with extreme temperatures. However, neither laboratory nor field results suggested that thermoregulatory behavior was overridden by feeding behavior, even though zooplanktonic food was more abundant in the outfall area than in unheated parts of the littoral zone.

Introduction

The Problem Rapid expansion of the steam-electric power industry has spurred concern for the potential impact of thermal effluents on aquatic ecosystems. At present rates of expansion, as much as one-fifth of the total freshwater runoff in the United States will be needed for steam-electric cooling water by 1980 (Krenkel and Parker, 1969). An increasing proportion of electrical power will be supplied by nuclear power stations; these produce more wasted heat per kilowatt of electricity generated than do fossil-fuel plants. The responses of aquatic organisms to thermal loading of their environment must be understood if we are to maintain environmental quality and plan effectively for growth of the power industry.

Fishes are profoundly affected by temperature. Extensive bibliographies by Raney and Menzel (1969) and Kennedy and Mihursky (1967) attest the wealth of available information regarding direct and indirect actions of temperature on the survival, growth, metabolism, behavior, and reproduction of fishes. Yet, ecological study of fishes in habitats heated by power plants began only about ten years ago in this country, and such investigations are still few and incomplete. Coutant (1970), in reviewing both published and unpublished information on "thermal pollution," concluded (p. 376):

> "Most power plant surveys lack detail of observation and definition of goals sufficient to provide more than circumstantial evidence for ecological processes...

> laboratory experiments are often unrealistic simulations of complex phenomena. True predictability will require judicious application of data from both sources."

This investigation sought to avoid the deficiencies mentioned by Coutant (1970) and, in so doing, contribute to knowledge of the ecological processes that occur in aquatic habitats receiving heated effluent.

The standpoint

Behavioral regulation of environment has been an underemphasized feature in the ecology of fishes. Fishes are mobile organisms, able to swim through their habitat at sustained speeds of a few body lengths per second (Bainbridge, 1960). If the potentially available environment is heterogeneous in quality, a fish can behaviorally regulate the conditions it must experience by spending more time in one subset of environment and less or no time in other subsets.

Temperature heterogeneity of some aquatic habitats is greatly increased by their reception of heated effluents from steam-electric plants. Although the fraction of habitat near the point of effluent discharge (outfall area) may be warmed by several degrees Celsius, temperatures throughout most of the receiving water mass typically are unaltered. For example, about 0.3% of Lake Monona's surface is warmed more than 1 C by effluent from a power plant; the percentage of total volume so warmed is much smaller.

In a habitat partly heated by thermal effluent, then, temperatures experienced by fishes depend on where they live within the habitat. If the fishes were randomly moving particles, the number exposed to elevated temperatures and the time each individual is exposed would be small. Fishes typically are not randomly distributed within a habitat; rather, they tend to be concentrated in some areas and scarce or absent in others.

Thus, the effects of steam-electric power production on fishes must depend first on their behavioral responses to elevated temperatures and to other features of the outfall area. It matters little whether in the laboratory yellow perch, for example, can grow at 30 C or can survive 33 C for 1000 min--if yellow perch never occur in an outfall area where temperatures exceed 29 C. The more important question is whether yellow perch given a choice will invade water of a particular temperature, and if so, for how long and for what reasons, ecologically prudent or otherwise. Only when fish are likely to occur voluntarily or by necessity under certain conditions does it become ecologically important to know the consequences of that exposure--consequences relative to survival, growth, and reproduction.

Major Objectives

Our conviction that the responses of fishes to environmental variation are first manifest in their distributions prescribed the primary goals of this investigation. Major objectives were

1. to assess spatial and temporal aspects of fish distribution in the outfall area of a steam-electric power plant,
2. to assess growth rates of young fishes in the outfall area,
3. to relate fish distributions to temperature by measuring the temperatures at which fishes live during summer in the outfall area,
4. to evaluate the relationship between fish distributions during summer and behavioral thermoregulation, and
5. to explore the extent to which fish may alter thermoregulatory behavior in order to acquire an essential resource--food.

Pursuit of these objectives required an integrated program of investigation in field and laboratory. First, fish distributions in the field were surveyed both day and night over the course of one year. Then followed more intensive effort to determine temperature distributions of fish in the outfall area during summer. Simultaneously, behavioral

thermoregulation of representative fishes was investigated in the laboratory.

Statistical treatment of data

To analyze data from both field and laboratory, non-parametric techniques were used almost exclusively. Reasons for avoiding more traditional, parametric methods included

1. uncertainty about the level of measurements (in most cases, the data probably were of ordinal strength),
2. uncertainty about the shapes of the sampling distributions, and
3. small sizes of samples.

Confidence intervals for medians were constructed in accordance with the method suggested by Mood and Graybill (1963; p. 406). All other non-parametric tests used in this work were described by Siegel (1956). Infrequent recourse to parametric statistics is indicated by the word "parametric" and follows the usage of Steel and Torrie (1960).

PART I

FIELD RESEARCH SITE: LAKE MONONA

Lake Monona (Dane County, Wisconsin) provides water for cooling the condensers of a coal and gas fired power plant (220 Mw) operated by the Madison Gas and Electric Company. Water is removed from the lake (1400 ha; max depth, 22.5 m) at two points, each 5 m below the surface and about 110 m offshore. After a 10 C rise in temperature during circulation through the condensers, water is returned to the lake at two surface outfalls located about 200 m apart on the shoreline. Heated effluent flows almost continuously from the primary outfall but does not flow from the secondary outfall during periods of low power production. A steel-slatted baffle at the secondary outfall diffuses the jet; the primary jet is unobstructed. Operating capacities of the circulation pumps total 6850 liters/sec, about 1.6 times the lake's average discharge rate (Hoopes, Zeller, and Rohlich, 1968).

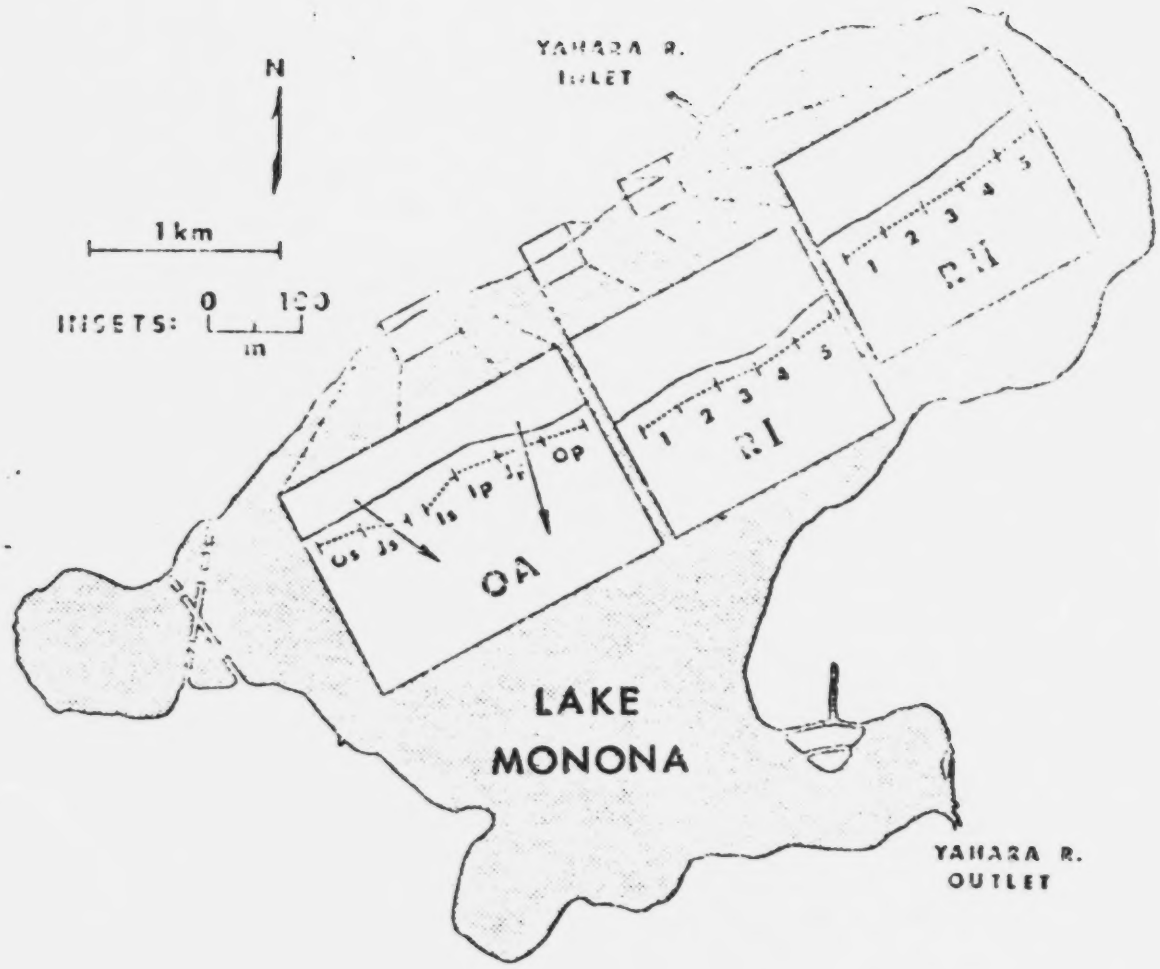
The heated discharge produces an area considerably warmer than the shallow water along the remainder of the shoreline. The heated area is about 1 ha in area and mostly less than 2 m deep.

During winter, a plywood baffle supported by floating booms extends 2.5 m beneath the surface to partially confine the heated discharge to an area of about 4.5 ha. In mid-winter, the baffled area is entirely free of ice except during the coldest weather.

Research effort was concentrated in the littoral zone of Lake Monona near the effluent outfalls (outfall area = OA) and in two reference areas (Figure 1). Reference areas I and II (RI and RII) were located about 600 m and 1300 m northeast of the outfall area. The sites selected for reference areas were more similar to the outfall area in bottom slope and type, aquatic vegetation, and exposure to winds than other locations in the lake. Yet, certain differences were apparent. Reference areas had more sand and less coarse gravel and rubble than the outfall area. The bottom in the outfall area was also more irregular and had a steeper slope. A channel about 2.5 m deep extended out from the primary outfall. The secondary jet passed over a sandy bar (0.6 m deep) approximately 40 m offshore. The dominant macrophyte in outfall and reference areas was watermilfoil (Myriopyllum), which sometimes was covered with growth of the filamentous alga, Cladophora. However, the reference areas had more wild celery (Vallisneria) and common Elodea (Elodea) than the outfall area.

Sixteen sampling transects were established in the study areas--five transects in each reference area and six in the outfall area (Figure 1). Each transect, 50 m long, was located parallel to shore and along the 1-1.5 m bottom-contour interval. Transects Js and Jp spanned the secondary and primary jets, respectively; the other transects in the outfall area were

Figure 1. Map of Lake Monona showing enlarged views of the outfall area (OA) and reference areas (RI and RII) with code letters for individual 50 m sampling transects (O_s, J_s, ..., RII 5). Arrows indicate positions of the secondary jet (across transect J_s) and primary jet (across transect J_p).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positioned inside (Is and Ip) and outside (Os and Op) the area bounded by the jets. Transects were marked at each end by numbered buoys or by structures on shore.

WATER TEMPERATURE IN THE STUDY AREAS OF LAKE MONONA

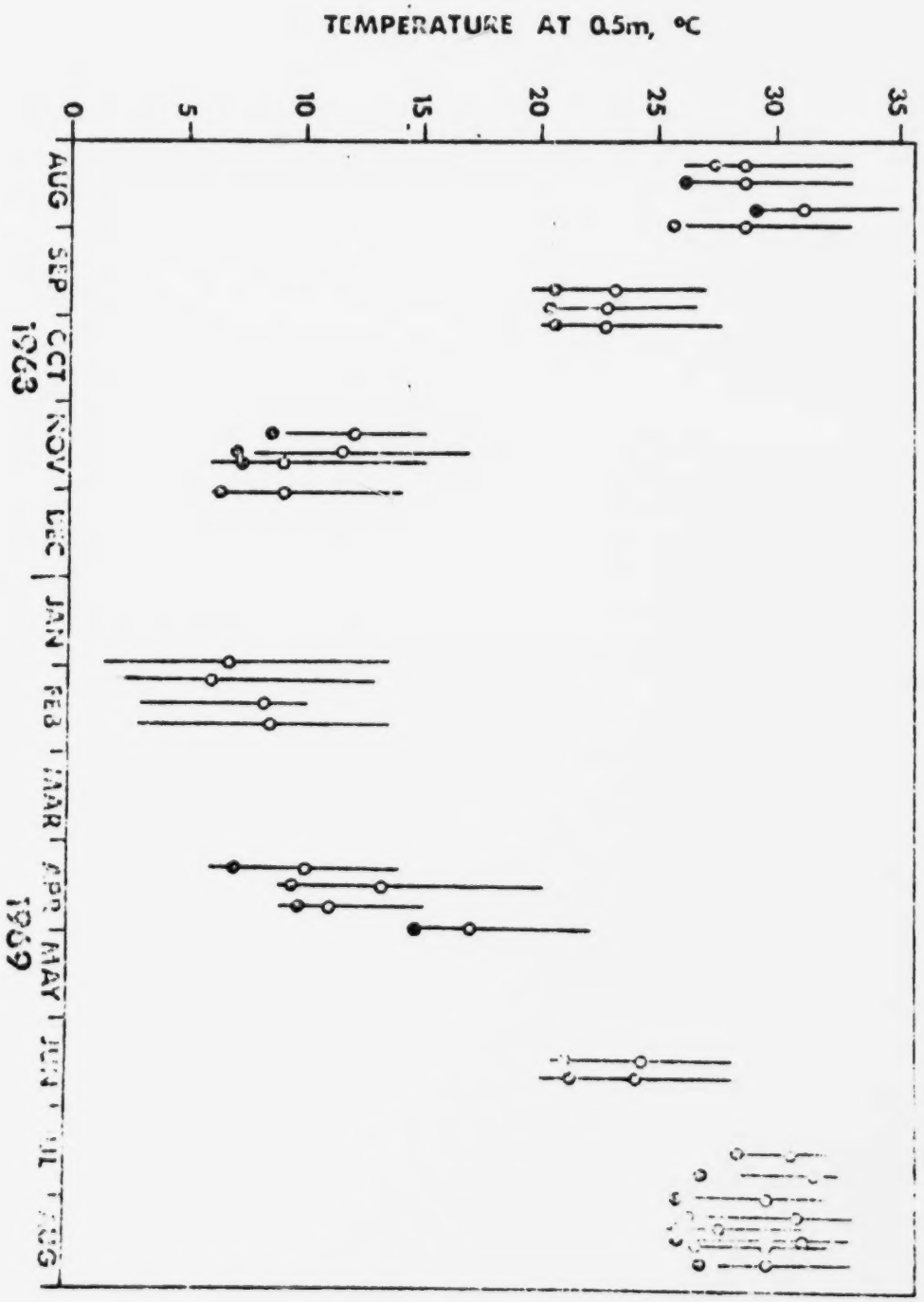
Water temperatures were systematically measured during each phase of the investigation of fish distribution. As fishes were sampled, temperatures 0.5 m below the surface were continuously recorded with a Rustrak Thermister Probe Recorder (Model 133). Temperatures at other depths were measured with an electronic thermometer of the Wheatstone Bridge type.

Water temperatures (0.5 m) in the reference areas were between 25 and 30 C on sampling dates in August 1968 and, following the winter minimum, returned to similar levels in July and August 1969 (Figure 2). The two reference areas had essentially identical temperatures. Minimum recorded temperature in the outfall area was similar to reference area temperatures on each date. However, median and maximum temperatures in the outfall area exceeded reference area temperature by 2-4 C and 6-8 C, respectively, on most sampling dates. Temperatures at night were generally less than 2 C below those recorded during the afternoon on the same date.

Median temperatures of transects on the same afternoon or evening varied less than 1 C within the reference areas but as much as 8.5 C in the outfall area. The transect across the primary jet (J_p) was 4-8 C warmer than the reference areas. Temperatures between the two jets (I_p and I_s) were often fairly

Figure 2. Median temperatures of the outfall area (open circle) and reference areas (solid circle) and range of temperature in the outfall area (vertical line) recorded at 0.5 m beneath the surface during each afternoon of electro-fishing, 8 August 1968 to 21 August 1969.

10a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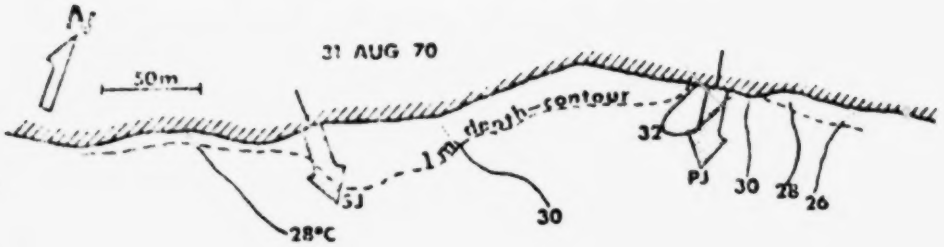
uniform and 3-5 C higher than those of reference areas. The transect across the secondary jet (J_s) was often cooler than that spanning the primary jet, even when heated effluent was flowing from the secondary outfall. Outside the jets, water temperature abruptly approached that of the reference areas.

Although some locations in the outfall area were consistently warmer than others, distribution of temperature varied greatly from day to day (Figure 3) because of changes in wind velocity and variation in rates of effleunt discharge. For example, on two consectuive dates (mid-afternoon) about 18% and 66% of water at 0.5 m depth in the outfall area was warmer than 30 C (Figure 3, 1 and 2 September 1970).

The outfall area was vertically stratified with respect to temperature. Although water 0.5 m beneath the surface was usually less than surface water, water temperature at 1 m was often 3 C lower than at 0.5 m. (Surface and 1 m temperatures in the reference areas seldom differed by even 1 C.) Vertical stratification, always poorly defined near the jets, deteriorated throughout the outfall area when strong onshore winds promoted mixing.

Figure 3. Distribution of temperature (°C) at 0.5 m beneath the surface in the outfall area on five successive afternoons, 31 August-4 September 1970. Secondary (SJ) and primary (PJ) jets are indicated by arrows in the upper diagram.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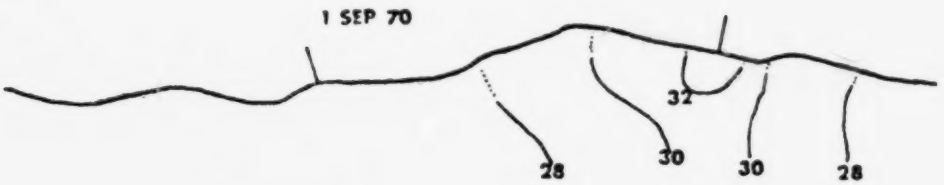
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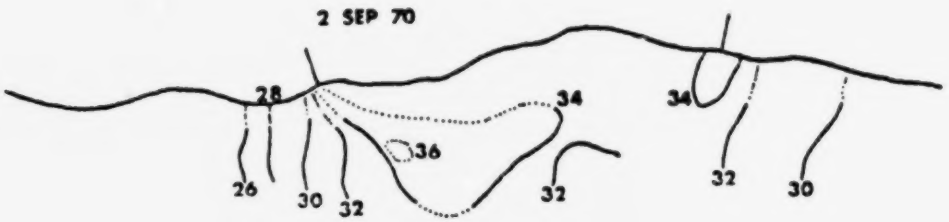
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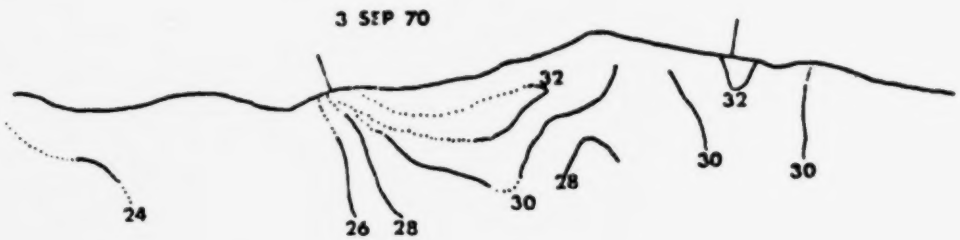
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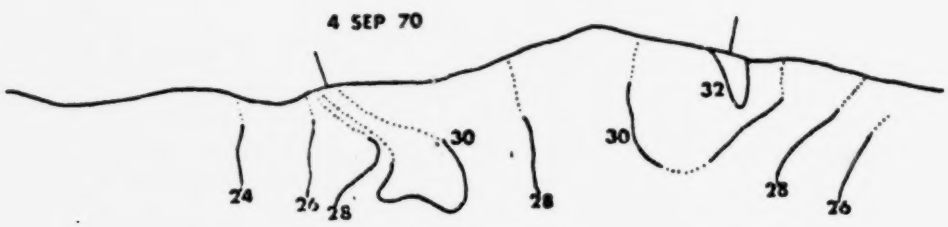
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DISTRIBUTION OF FISHES AMONG THE STUDY AREAS OF LAKE MONONA

Objectives

Abundances of fishes in each study area were estimated by electro-fishing. Objectives of the electro-fishing surveys were to determine whether the different fishes of the littoral zone were relatively concentrated or scarce in the outfall area and whether the degree of concentration varied from day to night and from season to season.

Sampling gear, procedures, and schedule

Fishes were captured with an electro-fishing apparatus mounted on a pontoon barge. Electricity (220 v a-c, 60 Hz) was supplied by a gasoline powered generator to three electrodes made from copper tubing 2.5 cm in diameter. The electrodes were suspended from booms projecting from the front of the barge; each electrode was weighted so that it hung vertically 1.4 m into the water. Immediately behind the electrodes, a push-net with a 1 x 1.3 m rectangular opening collected stunned fishes from the top meter of water; the 2.5 m long net of 6 mm mesh netting was lined in the final 1 m (purse) with 3 mm mesh netting.

The sampling unit was one electro-fishing run along a transect. During each run--which lasted 30-60 sec--water temperature 0.5 m beneath the surface was continuously recorded, and water depth was measured several times.

Generally, all fishes were removed from the net and either preserved in a 4% solution of formaldehyde or immediately identified, measured (total length), and released. However, catches of young-of-the-year (YOY) bluegills (Lepomis macrochirus) were so large during summer and early fall of 1968 that to preserve all of them was impractical and some were discarded.

Most larger fishes to be released were marked, in 1968, by a fin-punch distinctive for the area of capture or, in 1969, by a numbered anchor tag (Floy Anchor Tag, FD-67). The nylon "T"-barb of the anchor tag was inserted in the epaxial musculature beneath the dorsal fin of the fish.

Fish distributions were surveyed on 30 dates from 8 August 1968 to 21 August 1969. Transects were sampled twice on every date once during the afternoon (1230-1730 CST) and again after dark (1830-2400 CST).

Analytical treatment of fish-catch data

Analyses of distributions were based on catch per unit effort (catch/effort). Catch data were categorized by species, length class, season, time of day, and location of capture. Individuals of each species were pooled into one, two, or three length classes, the number of classes increasing with the number of specimens (Table 1). Two length classes approximately separated yearling and younger fish from those older than one year; three length classes approximately separated YOY, yearling, and

over-yearling fish. Sampling dates clustered temporally and thermally into seven seasonal periods: 1) August 1968, 2) September-October 1968, 3) November 1968, 4) January-February 1969, 5) April 1969, 6) June 1969, and 7) July-August 1969 (Figure 2). The minimum and maximum time intervals between successive sampling dates of any period were three and nine days, respecitvely. Within each season, day and night catches were considered separately.

Catch having first been stratified by species, length class, season, and time of day--catch/effort from the outfall area was compared statistically with that from the combined reference areas. The null hypothesis that catch/effort from the outfall area equalled catch/effort from the reference areas was assessed by application of the Kolmogorov-Smirnov one-sample test, a distribution-free analysis for goodness-of-fit. Statements concerning different abundances of fishes between areas are inferences based on significant ($p _ 0.05$) differences in catch/effort.

Abundance of fishes in the outfall area relative to reference area

Numbers captured of most fishes varied greatly with season and time of day. Young fishes were represented mostly in summer and fall samples; larger individuals of many species were caught at night more frequently than during the afternoon. Comparisons of catch/effort between outfall and reference areas were obviously limited to those seasonal-diel periods when the subject of

Table 1. Species, lengths, and numbers of fish caught from the study areas of Lake Monona during electrofishing surveys, 8 August 1968 to 21 August 1969.

Species		Length Class Identification	Range of Total Lengths, mm	Total Number Caught
Common Name	Scientific Name			
Longnose gar	Lepisosteus osseus (Linnaeus)	-	565-846	43[1]
Northern pike	Esox lucius Linnaeus	-	229-531	2
Carp	Cyprinus carpio Linnaeus	small	8-123	160
"	"	large	163-737	96
Golden Shiner	Notemigonus crysoleucas (Mitchill)	-	17-115	21
Emerald Shiner	Notropis atherinoides Rafinesque	-	80	1
Spottail Shiner	Notropis hudsonius (Clinton)	-	98-100	3
Bluntnose Minnow	Pimephales notatus (Rafinesque)	-	17-68	20
White Sucker	Catostomus commersoni (Lacépède)	-	403-460	4
Bigmouth Buffalo	Ictiobus cyprinellus (Valenciennes)	-	440-600	7
Black Bullhead	Ictalurus melas (Rafinesque)	small	33-150	165
"	"	large	151-265	46
Yellow Bullhead	Ictalurus natalis (Lesueur)	-	226-245	2
Brown Bullhead	Ictalurus nebulosus (Lesueur)	-	63-230	12
Banded Killifish	Fundulus diaphanus (Lesueur)	-	53-64	2
Brook Silverside	Labidesthes sicculus (Cope)	-	8-97	413
Brook Stickleback	Culaea inconstans (Kirtland)	-	29	1
White Bass	Morone chrysops (Rafinesque)	-	17-294	53
Yellow Bass	Morone mississippiensis Jordan and Eigenmann	small	13-50	417
"	"	medium	51-99	187
"	"	large	107-256	287

Table 1. (Continued)

Species		Length Class Identification	Range of Total Lengths, mm	Total Number Caught
Common Name	Scientific Name			
Rock Bass	Ambloplites rupestris (Rafinesque)	small	10-48	120
"	"	large	51-210	54
Green Sunfish	Lepomis cyanellus Rafinesque	-	19-166	17
Pumpkinseed	Lepomis gibbosus (Linnaeus)	small	12-75	149
"	"	large	76-170	136
Bluegill	Lepomis macrochirus Rafinesque	small	28-75	19154
"	"	medium	76-100	237
"	"	large	101-224	848
Largemouth Bass	Micropterus salmoides (Lacépède)	-	51-311	77
White Crappie	Pomoxis annularis Rafinesque	-	114-247	10
Black Crappie	Pomoxis nigromaculatus (Lesueur)	small	12-75	853
"	"	large	76-249	81
Iowa Darter	Etheostoma exile (Girard)	-	23-39	63
Johnny Darter	Etheostoma nigrum Rafinesque	-	65	1
Yellow Perch	Perca flavescens (Mitchill)	small	46-99	285
"	"	large	101-286	99
Log Perch	Percina caprodes (Rafinesque)		35-117	44
Walleye	Stizostedion vitreum vitreum (Mitchill)	-	13-535	41
Freshwater Drum	Aplodinotus grunniens Rafinesque	-	68-420	53
Mottled Sculpin	Cottus bairdi Girard	-	31-83	93

[1]Includes sighted as well as captured longnose gar.

comparison was caught in numbers sufficient for meaningful statistical interpretation. Comparisons between areas were automatically precluded for the January-February 1969 period because the reference areas were not sampled.

Comparisons of catch/effort between outfall and reference areas show that of the 31 species collected, eleven were unevenly distributed between outfall and reference areas during at least one seasonal-diel period. Distributions of two of these eleven species are described below in detail.

Bluegills (Lepomis macrochirus) were caught much more frequently than any other species; 848 large (>100 mm), 237 medium-size (76-100 mm), and over 19,000 small (≤75 mm) specimens were taken.

Large and medium-size bluegills were more abundant by day in the outfall area than in the reference areas during August 1968, September-October 1968, November 1968, and July-August 1969. Large bluegills at night were more abundant in the outfall area than in the reference areas during all seasonal periods except August 1968 and July-August 1969 (Figure 4); at night, medium-size bluegills were more abundant in the outfall area than in the reference areas during August 1968, September-October 1968, and June 1969.

Small bluegills (≤75 mm) were more abundant, both day and night, in the outfall area than in the reference areas during August 1968 and July-August 1969, and, at least by day, in September-October 1968 and June 1969, as well (Figure 5).

Figure 4. Number of large bluegill caught from each electro-fishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.

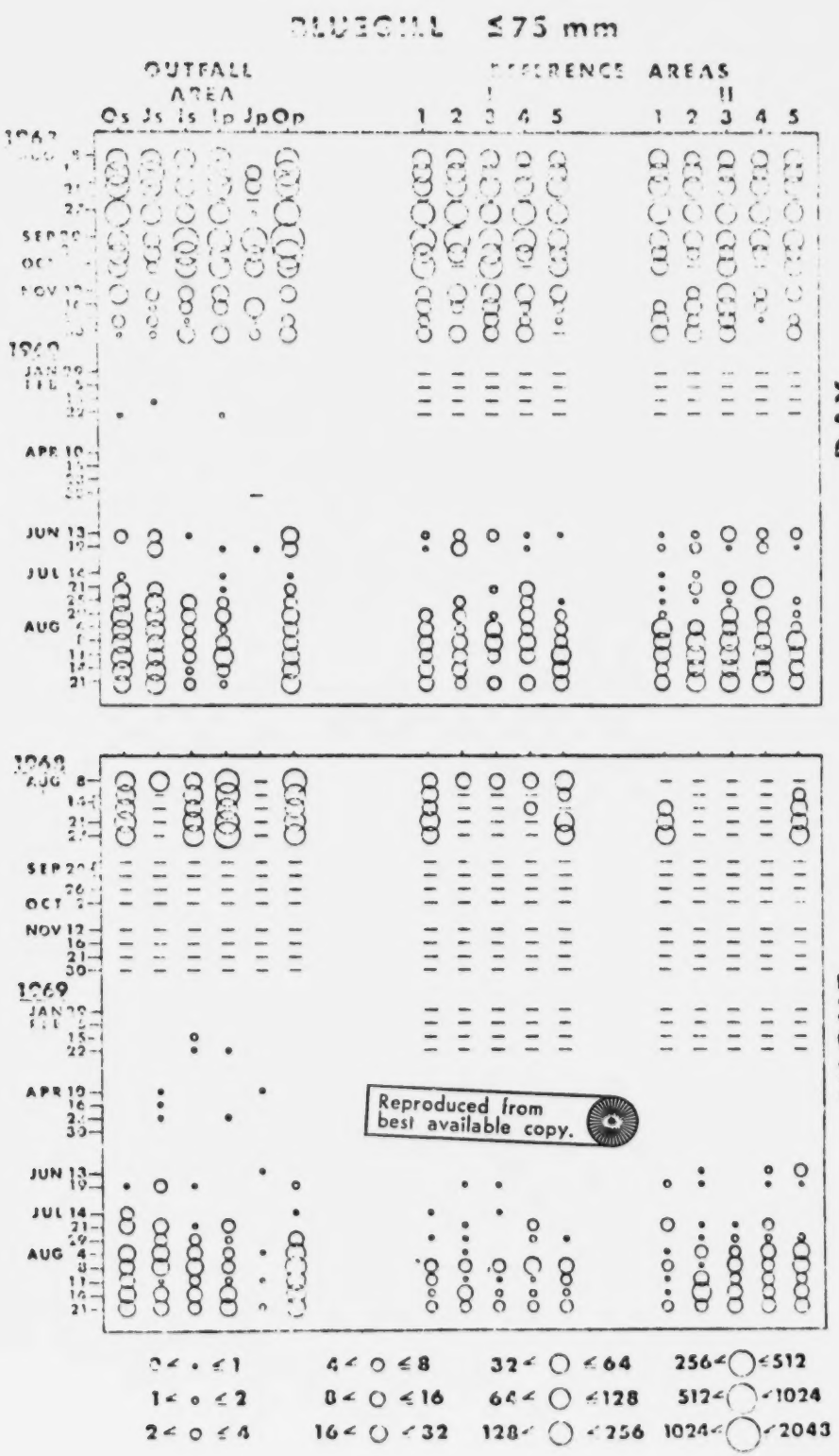
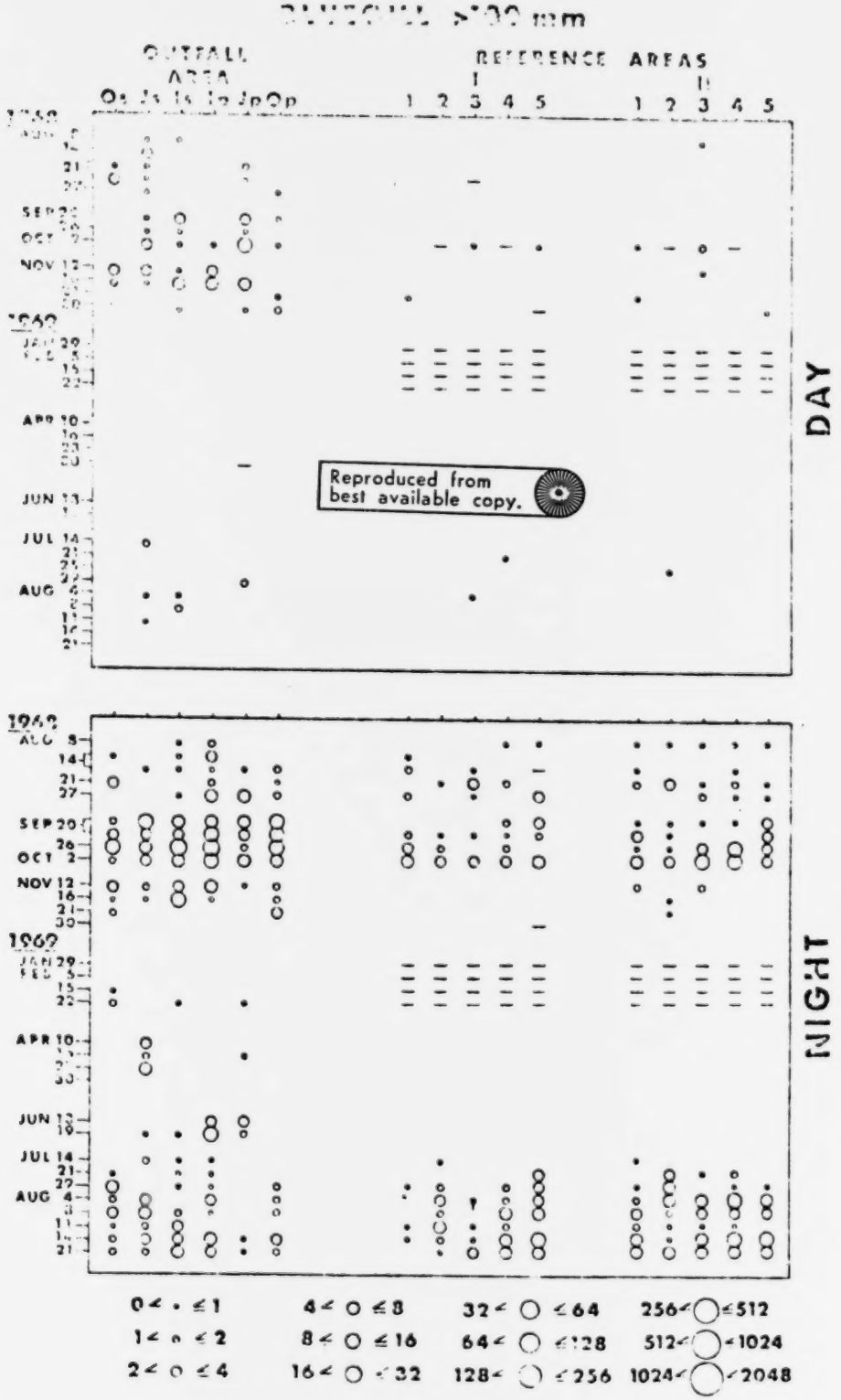

BLUEGILL ≤75 mm
OUTFALL AREA
REFERENCE AREAS
I
II
Os Js Is Ip Jp Op
1 2 3 4 5
1 2 3 4 5
1967
SEP
OCT
NOV
1968
JAN
FEB
APR
JUN
JUL
AUG
DAY
1968
AUG
SEP
OCT
NOV
1969
JAN
FEB
APR
JUN
JUL
AUG
NIGHT
Reproduced from best available copy.
0< • ≤1
1< o ≤2
2< o ≤4
4< O ≤8
8< O ≤16
16< O <32
32< O ≤64
64< O ≤128
128< O <256
256<◯≤512
512<◯<1024
1024<◯<2043

Figure 5. Number of small bluegill caught from each electro-fishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.


OUTFALL AREA
REFERENCE AREAS
I
II
1 2 3 4 5
1 2 3 4 5
1968
AUG
SEP
OCT
NOV
1969
JAN
FEB
APR
JUN
JUL
AUG
DAY
NIGHT
Reproduced from best available copy.
0< • ≤1
1< • ≤2
2< • ≤4
4< O ≤8
8< O ≤16
16< O ≤32
32< O ≤64
64< O ≤128
128< O ≤256
256< O ≤512
512< O ≤1024
1024< O ≤2048

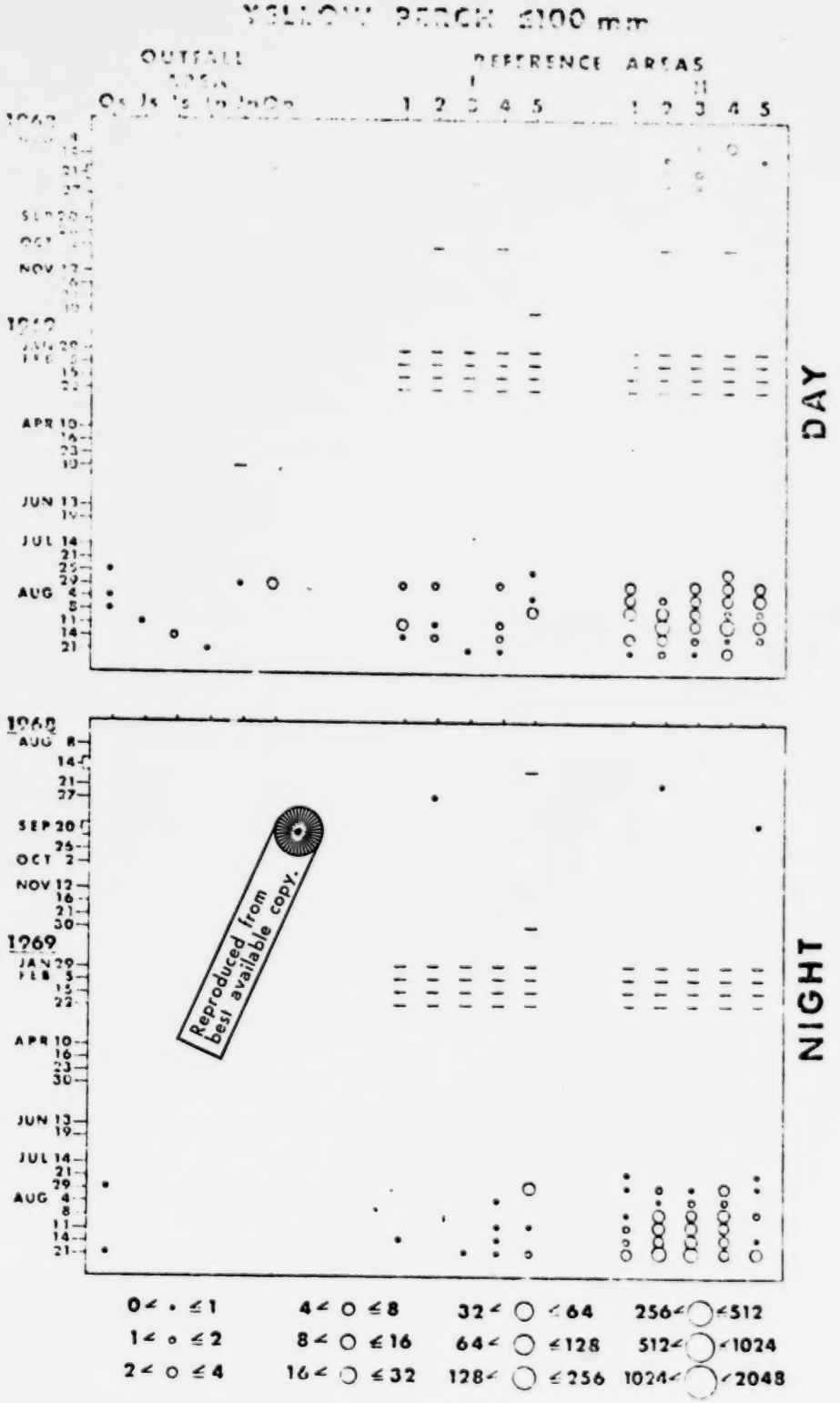
In November 1968, however, young bluegills during the day were more abundant in reference areas than in the outfall area.

Young-of-the-year bluegills were taken in progressively increasing numbers as summer advanced during both years, but mid-August catches in 1969 were only about 20% of those in 1968. Catch/effort in 1968 declined during November from the maximum reached in September. Reference Area I produced a much smaller fraction of the total young bluegill catch in July-August 1969 than in August 1968 (Figure 5).

Yellow perch (Perca flavescens)--Few large yellow perch ($\geq$100 mm) were taken, except at night during April 1969. All of these were caught from the reference areas; RII produced more fish than RI. All specimens examined were ripe males. Yellow perch egg masses were frequently observed during April in both reference areas. Small yellow perch ($\leq$100 mm) were more abundant in the reference areas (primarily RII) than in the outfall area during both day and night in July-August 1969 (Figure 6).

The extent to which littoral distributions of Monona fishes were biased in favor of or against the outfall area may be summarized by segregating several response types. Segregation is achieved by a dichotomous key used in the same manner as those constructed for taxonomic identifications:

Figure 6. Number of small yellow perch caught from each electro-fishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.


YELLOW PERCH ≥100 mm
OUTFALL
REFERENCE AREAS
1 2 3 4 5 1 2 3 4 5
1968
SEP 20
OCT
NOV 12
1969
APR 10
JUN 13
JUL 14
AUG
DAY
NIGHT
Reproduced from best available copy.
0< • ≤1
1< o ≤2
2< o ≤4
4< O ≤8
8< O ≤16
16< O ≤32
32< O <64
64< O ≤128
128< O ≤256
256< O ≤512
512< O <1024
1024< O <2048

1a Catch/effort not significantly different between outfall and reference areas during any seasonal diel period.....2

1b Catch/effort significantly different between outfall and reference areas during at least one seasonal-diel period....3

2a Fewer than 20 specimens caught during any seasonal-diel period..... Rare Types

Northern pike	Blk. Bullhead, large	Brook stickleback
Golden shiner	Yellow bullhead	Green sunfish
Emerald shiner	Brown bullhead	White crappie
Spottail shiner	Banded killifish	Johnny darter
Bluntnose minnow	White bass	Walleye
White sucker	Rock bass, large	Freshwater drum
Bigmouth buffalo		

2b At least 20 specimens caught during some seasonal-diel period.....Indifferent Types

Carp, small	Iowa darter	Log perch
Pumpkinseed, large	Black crappie, large	

3a Catch/effort in the reference areas never significantly less than in the outfall area.....Reference-Area Types

Black bullhead, small	Yellow bass, medium	Yellow perch, large
Yellow bass, small	Yellow perch, small	Mottled sculpin

3b Catch/effort in the reference areas significantly greater than in the reference areas during at least one seasonal-diel period.....4

4a Catch/effort in the reference areas significantly greater than in the outfall area during at least one seasonal-diel period.....Mixed Types

Bluegill, small	Black crappie, small

4b Catch/effort in the outfall area never significantly less than in the reference areas.....Outfall-Area Types

Longnose gar	Rock bass, small	Bluegill, Large
Carp, large	Pumpkinseed, small	Largemouth bass
Yellow Bass, large	Bluegill, medium	

The key perhaps misrepresents the responses of some fishes. Small carp were probably more abundant during summer in the reference areas. Small bluegills were more abundant in the reference areas in November 1968, but were more abundant in the outfall area during

during most other seasons. Large black crappies were probably more abundant in outfall than in reference areas during September-October 1968. Thus, small carp may have been a reference-area type, whereas both small bluegills and large black crappies were probably outfall-area types.

There were no reference data with which to compare catches in the outfall area during January-February 1969, but electrofishing and visual observation suggested that fishes present in the outfall area were few compared with numbers there at other seasons. Twenty-four day and 24 night runs yielded only 31 specimens representing six species--13 bluegills, 10 brook silversides, 3 Iowa darters (Etheostoma exile), 2 carp, 2 golden shiners (Notemigonus crysoleucas), and 1 yellow bass. Aquatic vegetation was essentially absent from the entire outfall area during winter.

Recapture of marked fishes

Although 934 fish were fin-punched during 1968 and 1726 more were tagged in 1969, we had recaptured only eight marked specimens by 1 July 1970. Forty-two tagged specimens were caught and reported to us by fishermen. Of 14 yellow bass and 21 bluegills reported by fishermen, 10 and 12 fish, respectively, were caught more than 1 km from the tagging location. These data verified that we were not catching and recatching the same individuals. They also supported our general impression that residence times of larger fishes in the sampling areas were short--one week or less.

Distribution of Monona fishes compared with distribution of fishes in other waters receiving heated effluent

Little published literature exists on the distributions of fishes in other waters receiving heated effluent (Coutant, 1970; Raney and Menzel, 1969). No published field study and only a fraction of the report literature with which we are acquainted deal with a lake environment or an ichthyofauna very similar to that of Lake Monona. However, most information now available suggests that, whatever the habitat type and ichthyofaunal composition, some species avoid effluent outfall areas while others concentrate there. Alabaster and Downing (1966) observed that fish distributions were little altered by effluents which warmed only the surface layers of several British rivers; but, in the more thoroughly mixed River Trent, bream (Abramis brama), tench (Tinca tinca), and carp lived in the warmest water available (about 28 C), while roach (Rutilus rutilus) and gudgeon (Gobio gobio) avoided water warmer than 26 C. Trembly (1961) reported that satinfin shiners (Notropis analostanus), banded killifish (Fundulus diaphanus), American eels (Anguilla rostrata), redbreast sunfish (Lepomis auritus), and bluegills occurred during summer at temperatures above 32 C in the effluent lagoon of a power plant on the Delaware River (Pennsylvania). During cooler weather, the lagoon was inhabited by additional species, including golden shiner, brown bullhead (Ictalurus nebulosus), largemouth bass, black crappie, pumpkinseed, and rock bass. During summer in the Wabash River (Indiana), carp, buffalo

(Ictiobus sp.), longnose gar, and channel catfish (Ictalurus punctatus) were among species concentrated below a heated effluent outfall (>30 C), but river carpsuckers (Carpiodes carpio), redhorses (Moxostoma sp.), spotted bass (Micropterus punctulatus), longear sunfish (Lepomis megalotis), and sauger (Stizostedion canadense) were more abundant upstream from the outfall (Gammon, 1971). Carp, buffalo, and channel catfish--but also river carpsuckers and longear sunfish--occurred in summer at temperatures exceeding 33 C in an effluent canal discharging into the White River in Indiana (Proffitt, 1969). Threadfin shad (Dorosoma petenense), sauger, skipjack herring (Alosa chrysochloris), and channel catfish concentrated in a heated discharge harbor on Kentucky Lake, Tennessee, during winter and spring (Dryer and Benson, 1957). In marine environments, too, some fishes apparently concentrate near heated discharge outfalls while others seem less abundant than in unheated areas (Allen, Boydstun, and Garcia, 1970).

We are aware of no quantitative information on the distributions of young fishes relative to heated discharges, except for those data we collected in Lake Monona, nor have nocturnal distributions of fishes at other sites been investigated. Whether size and diel differences like those observed in Monona are typical of fish distributions in heated environments is unresolved.

Three field studies (Trembley, 1961; Proffitt, 1969; Dryer and Benson, 1957) suffered a common deficiency: Suitable

reference sites, with which the discharge area could be compared, were unavailable. Therefore, responses of fishes to the discharge area at one season could only be judged by those during some other season or reconciled with general impressions of fish distributions in the body of water as a whole. Thus, ". . . a remarkably common phenomenon, i.e., the attraction of fish to warmed water [from power plants] during cooler months and repulsion by thermal extremes in the peak of summer" (Coutant, 1970; p. 367) must be interpreted with some caution.

Whatever occurs seasonally in heated discharge areas may also occur simultaneously in other similar, but unheated, parts of the habitat. For example, apparent abundances of several fishes (e.g., bluegills) fluctuated seasonally in the outfall area of Lake Monona, but similar fluctuations occurred simultaneously in the reference areas. Ratios of outfall to reference area catch/effort fluctuated to a lesser extent. Only among small bluegills and small black crappies were these significant reversals in the ratio from one season to another. In the crappies, reversal occurred from one summer to the next, a change which could not be attributed to temperature. Young bluegills were more abundant in the outfall area during both summers but were more abundant in the reference areas during a colder season, November 1968. In Lake Monona, fishes did not differentially avoid the outfall area during summer to a much greater extent than at other seasons. Nor were the numbers

of fish present in the outfall area during January-February 1969 likely to have been as great as numbers in summer.

Whatever difficulties arise in the assessment of fish abundances in outfall areas in the absence of suitable control sites, there can be little doubt that some spectacular concentrations of fishes do occur in direct response to the operation of power plants. For example, Dryer and Benson (1957) observed fish concentrations during winter and spring in a heated discharge harbor on Kentucky Lake, Tennessee; threadfin shad were so abundant that they hampered boating by clogging the cooling systems of outboard motors. But even this example is somewhat confusing--shad also concentrated in the unheated inlet harbor, clogging the intake screens of the power plant's cooling system.

SIZE DISTRIBUTIONS OF YOUNG-OF-THE-YEAR BLUEGILLS IN THE STUDY AREAS OF LAKE MONONA

Objectives

To determine if sizes of YOY bluegill differed among outfall and reference areas, lengths and weights were obtained from specimens collected during electro-fishing surveys of 1968 and 1969. By comparing sizes of fish caught on successive sampling dates from each area. We hoped to ascertain whether or not young bluegill grew at different rates in outfall and reference areas.

Length-frequency distributions of YOY bluegills.

Samples of preserved fish were examined to determine if distributions of fish length varied among study areas.

Adequate sample sizes (generally 20 or more fish) allowed interareal comparison of bluegill length distributions on several dates during summer and fall 1968 and summer 1969.

Length distributions of YOY bluegills differed among outfall and reference areas, but the relationship among areas with respect to fish length changed from day to night. During afternoon in both 1968 and 1969, YOY bluegills from the outfall area were generally longer than those from either reference area; RI and RII fish had similar length distributions. The general increase in fish lengths as summer progressed was primarily the result of growth. Growth rates of YOY bluegills may have differed among areas, but any difference was obscured by other processes, particularly size-dependent movements of the fish.

The apparent importance of size-differential movements on diel changes in YOY bluegill length distributions suggested that persistent afternoon differences in fish lengths among areas were not entirely or even primarily due to interareal differences in growth rate. Larger YOY bluegills may have been attracted to the outfall area from adjacent areas. Certainly, larger catches of YOY bluegills from the outfall area than from reference areas implied active concentration of fish in the outfall area. It seems reasonable that larger fish, being more mobile than smaller fish, would have been differentially concentrated.

In no other system receiving thermal effluent have length distributions of YOY fishes been investigated. Here, Monona fish are compared with those from lakes not receiving heated effluent.

Median lengths of Monona YOY bluegills caught during afternoon increased at rates commensurate with those observed for other populations--about 0.5 mm/day. YOY bluegills measured by Krumholz (1949) increased between 12 and 25 mm total length at 0.1 mm to 0.6 mm/day. Werner (1969) estimated that young bluegills grew 0.4 mm/day in an Indiana hatchery pond. But, on August 14 during both 1968 and 1969, YOY bluegills from Monona were 3-5 mm shorter than a 10-year average computed for YOY bluegills in Clear Lake, Iowa (Ridenhour, 1960).

On 14 August 1969, Monona YOY yellow bass were about 5 mm shorter but YOY black crappies about 5 mm longer than 10-year averages for these species on 14 August in Clear Lake, Iowa (Ridenhour, 1960).

Although the authors just cited have assumed that changes in average length of fish from date to date were due primarily to growth, their data, like those from Monona, were potentially confounded by length-dependent recruitment, mortality, and movements of the fish.

Length-weight relationships of YOY bluegills

Length-weight relationships of bluegills were examined for evidence of differences in condition between fish in outfall and reference areas.

Specimens collected during four afternoons in 1968 and during afternoons and evenings of three dates in 1969 were removed individually from the preservative, blotted on a paper towel, weighed, and then measured.

TEMPERATURE DISTRIBUTIONS OF FISHES IN THE OUTFALL AREA DURING SUMMER

Catch/effort with respect to water temperature

To generally relate fish distributions within the outfall area to temperature, the catch/effort data collected during August 1968 and July-August 1969 were examined for association with water temperature. Catch from each electro-fishing run in the outfall area was assigned the median temperature recorded during the run. The catch was then categorized by species, length class, year, and time of day. For each category of catch, catch/effort at each 0.5 C increment of temperature was computed. The resulting temperature distributions of catch/effort were analyzed for nonuniformity by application of the Kolmogorov-Smirnov one sample test, the level of significance having been set at 0.05. This analysis enabled identification of those fishes which tended to be more abundant at some temperatures.

Fishes occurred at virtually all available temperatures, but in several cases the distribution of catch/effort was significantly nonuniform with respect to median run temperature. Among fishes inferred to be not equally abundant at all temperatures, only longnose gar and medium-size yellow bass were biased toward temperatures higher than expected under the hypothesis of uniform distribution. Small rock bass, large pumpkinseeds, small bluegills, largemouth bass, small black crappies, and medium-size yellow perch were distributed at temperatures lower than expected; the same pattern

held for large carp during the day in 1968 and for large and medium-size bluegills at night in 1969. Small carp were concentrated at temperatures near 29 C during both day and night in 1969.

Fine-scale features of the temperature distributions of OA fishes were obscured by the large scale of sampling. Variation of temperature within a run limited resolution of capture temperatures to about 4 C. Fish caught at all points along a transect were assigned the median run temperature, but two, fish caught near either end of some transects (O_p, for example) may have been at temperatures 2-4 C lower and higher, respectively, than the median. Median run temperatures overestimated temperatures experienced by fish which stayed near the bottom, because bottom temperatures were usually lower than at 0.5 m where temperature was recorded.

Most studies of heated discharge sites have generally yielded inadequate data on the temperature distributions of fishes (Coutant, 1970). This has largely resulted from inability to measure, reliably and simultaneously, 1) water temperature where fishes actually live and 2) relative abundances of fishes within an area reasonably homogeneous except for variation in temperature.

Body temperatures of fishes with respect to water temperature

The analysis of catch/effort provided a coarse measure of the temperatures experienced by fishes in the outfall area.

During summer 1970, body temperatures of just-caught specimens were measured to obtain more accurate definition of fish distributions with respect to temperature.

Fishes were caught by the electro-fishing technique described above, except that stunned individuals were removed from the water by hand-held dip net. After each specimen was lifted from the water, its body temperature was measured within 40 sec (median time, 12 sec) and recorded along with total length of the fish, Central Standard Time, 0.5 m water temperature, and water depth.

Body temperatures were measured with a thermister-bridge circuit. The thermister was fixed in the tip of a 16-gauge hypodermic needle of stainless steel. The needle was inserted into the epaxial musculature beneath the dorsal fin of the fish to a point near the interneural spines (approximately halfway through the fish). The temperature measuring system arrived at thermal equilibrium within 3 sec after the needle entered the fish.

Sampling effort was expended on each of the following dates: 11, 13, 17, 19, 21 August 1970. Although the spatial distribution of effort was not regimented, the whole outfall area was electro-fished during each afternoon or evening of sampling. A concerted effort was made to take fishes from the entire spectrum of water temperature.

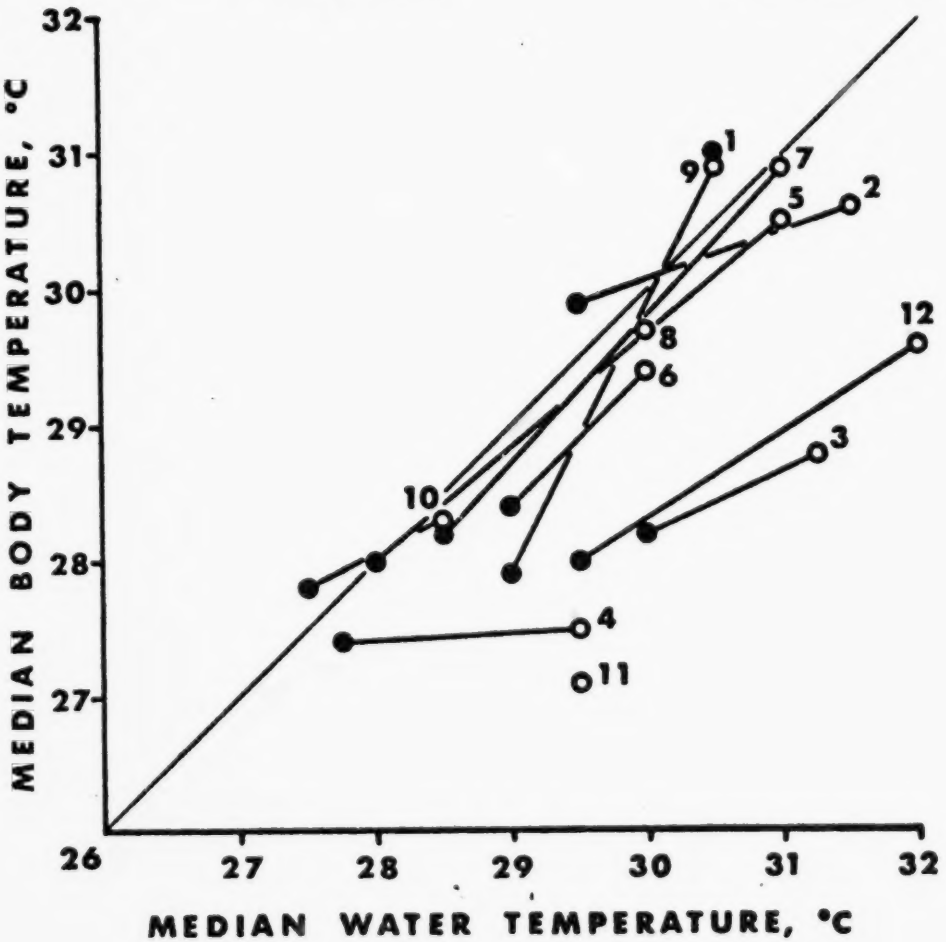
Body temperatures of most fishes tended to increase with water temperatures recorded at 0.5 m where they were captured (Figure 7). Some fishes had body temperatures consistently higher than those of others caught during the same diel period. Bluegills longer than 100 mm, largemouth bass longer than 100 mm, carp, and pumpkinseeds had median intramuscular temperatures above 30 C during the afternoon; in contrast, afternoon medians for yellow bass, black crappies, rock bass, and yellow perch were below 29 C. Except for longnose gar and carp with median body temperatures of 31.0 C and 29.8 C, respectively, median fish temperatures at night were between 28.4 C and 27.8 C, being highest for smaller bluegills and least for rock bass.

At night, both fish and capture temperatures were lower than during the afternoon; in fact, sample medians were lower at night in every case. Comparison of 95% confidence intervals for the medians indicated that body temperatures of five species at night were significantly lower than during the afternoon--bluegills, largemouth bass, pumpkinseeds, black crappies, and freshwater drum (Aplodinotus grunniens). However, median water temperatures at points of capture decreased significantly from afternoon to night only for larger bluegills and for pumpkinseeds.

Intramuscular temperatures probably estimated within 1 C the average of each specimen's "recent" thermal experience.

Figure 7 Median body temperature of fish and median water temperature at the places of capture for each of ten species of fishes caught in the outfall area during afternoon (open circle) and evening (solid circle), August 1970.

1 LONGNOSE GAR, 468-815 mm
2 CARP, 323-586 mm
3 YELLOW BASS, 145-234 mm
4 ROCK BASS, 98-182 mm
5 PUMPKINSEED, 100-161 mm
6 BLUEGILL, 53-99 mm
7 BLUEGILL, 100-193 mm
8 LARGEMOUTH BASS, 72-99 mm
9 LARGEMOUTH BASS, 100-408 mm
10 BLACK CRAPPIE, 126-249 mm
11 YELLOW PERCH, 73-188 mm
12 DRUM, 223-317 mm



Body temperatures were a better measure than capture temperature of where in the thermal environment fish actually lived. Variation of water temperature with depth rendered capture temperature a poor estimator of the temperatures experienced by some fishes, particularly those that lived near the bottom--yellow bass, rock bass, yellow perch, and freshwater drum (Figure 7). Yellow bass, which concentrated near the discharge jets, actually lived in relatively cool water near the bottom. In contrast, longnose gar spent much of their time near the surface at temperatures somewhat higher than those recorded from our thermister at 0.5 m. Several individual longnose gar, carp, and largemouth bass were 1-3 C warmer than the water from which they were caught; these fishes must have moved horizontally from warm water into cooler water just prior to capture. Similarly, relatively low body temperature of some specimens taken in the outfall area (particularly at night) suggested recent emigration from cool, deep water outside the outfall area.

Fish and capture temperatures were lower at night than during the day owing to 1) a general decrease in temperature of the outfall area at night, 2) movements of fishes away from the jets at night, and 3) a tendency for fishes to stay nearer the bottom at night. Whereas, processes 1) and 2) would have lowered both fish and capture temperatures, process 3) would have caused reduction in fish temperatures but not capture temperatures.

Temperature acclimation levels of young-of-the-year (YOY) bluegills

Young-of-the-year bluegills were by far the most abundant group of fishes in the littoral zone during summer. To evaluate the temperatures experienced in the outfall area by YOY bluegills, their levels of temperature acclimation were estimated by heat resistance tests.

Young bluegills, 20-70 mm long, were caught by 10 to 20 m long runs with the push-net (no electro-shock) from locations at either side of both jets. One sample of 50-60 fish was obtained from each of the four locations during early afternoon on each of five successive dates, 31 August-4 September 1970. During each collection run, water temperature 0.5 m beneath the surface was continuously recorded.

The fish were transported to the laboratory in styrofoam containers filled with Lake Monona water from outside the outfall area. They were held overnight in the containers. During this time, the temperature of the water in the containers changed from 23-26.5 C to ambient temperature in the laboratory, 21.5-24.0 C. The thermal experience of the fish after capture was, in all cases, at or below the minimum temperature recorded at capture.

On the day following capture, about 20 fish from each sample were transferred to a lethal temperature bath regulated at 36.5±0.05 C. Each bath contained 25 liters of continuously

aerated water form Lake Mendota (which discharges into Lake Monona through a 1.3 km segment of the Yahara River). Resistance time--the time between entry into the bath and death (cessation of gill movement)--was recorded for each specimen.

To relate resistance times of fishes from the outfall area to their level of temperature acclimation, the resistance time distributions for YOY bluegills of known temperature acclimation were obtained (Figure 8).

Median times of heat resistance (ranked within dates) varied significantly among locations within the outfall area (Friedman two-way AOV; $p < 0.02$). Young bluegills collected between the two jets had longer resistance times than their counterparts caught on the same date from outside the respective jets (Figure 9). Fish from each side of the primary jet differed more in heat resistance than those from each side of the secondary jet. Using data from all locations and dates, median heat resistance times were positively correlated (Kendall's $\tau = 0.44$; $p < 0.01$) with water temperature at the sites of fish collection. Water temperature within locations differed significantly among dates (Friedman two-way AOV: $p=0.05$); median resistance times did not (Friedman two-way AOV: $p=0.25$).

All samples of fish from the outfall area had median resistance times corresponding to those of fish acclimated between 29.4 and 31.3 C in the laboratory (cf. Figures 8 and 9).

Figure 8 Relationship of acclimation temperature and median time to death at lethal temperature (36.5 C) for samples of 10 young-of-the-year bluegills acclimated in the laboratory. Circles indicate samples held overnight at room temperature before resistance tests; triangles indicate samples tested immediately after removal from the acclimation temperature. The curve, fitted by eye to the circles, was used to estimate acclimation temperatures of fish from the outfall area (Figure 30).

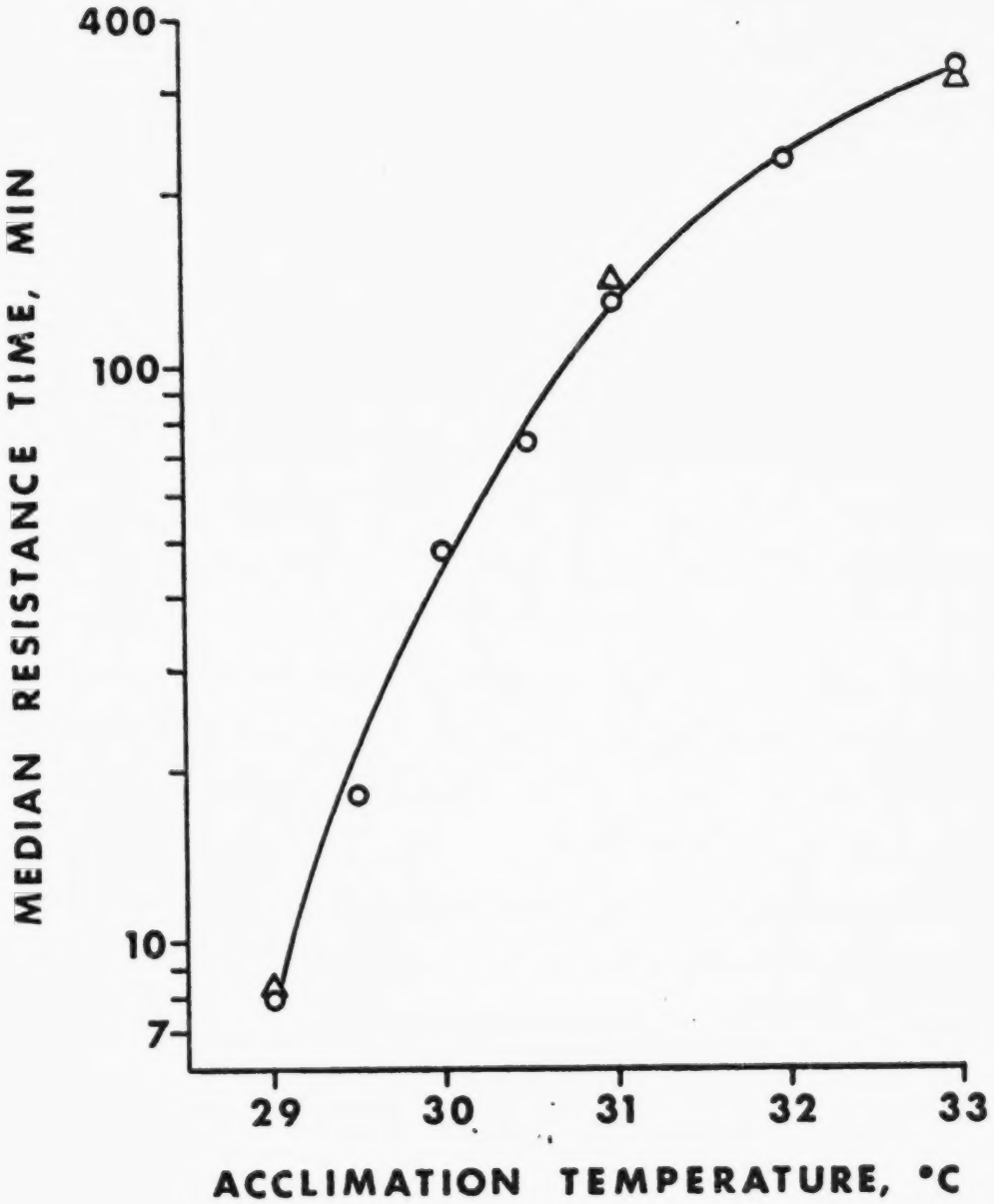
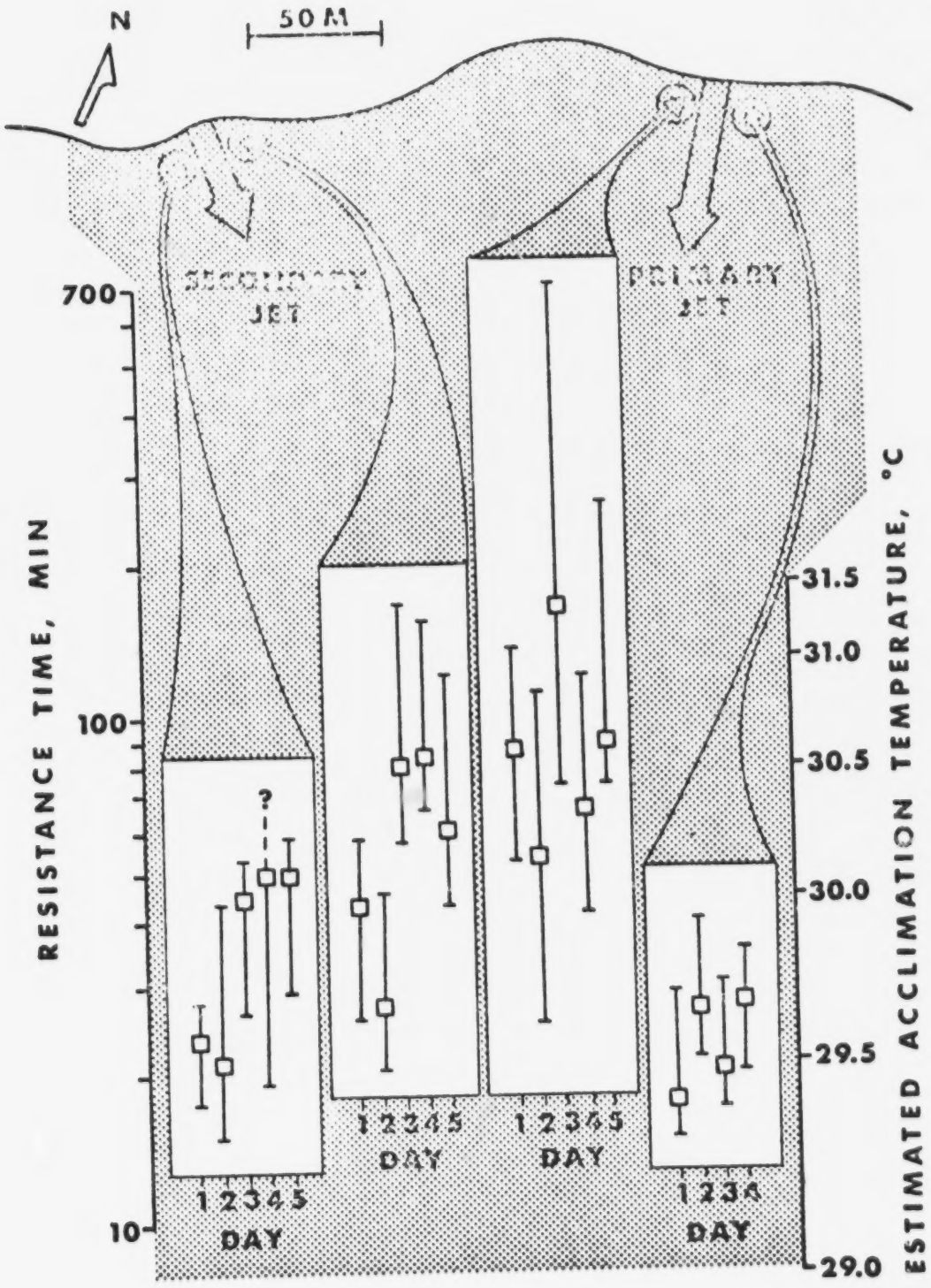

400
100
10
7
MEDIAN RESISTANCE TIME, MIN
29
30
31
32
33
ACCLIMATION TEMPERATURE, °C

Figure 9 Median (square) and interquartile-range (vertical line) of times to death at a lethal temperature (36.5 C) and estimated acclimation temperature (square) for each sample of about 20 young-of-the year bluegills from the outfall area, 31 August-4 September 1970. The data from each sample are grouped by location of sample collection and ordered within each group by date of sample collection (Day 1 = 31 Aug., ..., Day 5 = 4 Sep.).


N
50 M
SECONDARY JET
PRIMARY JET
700
100
10
RESISTANCE TIME, MIN
?
1 2 3 4 5
DAY
1 2 3 4 5
DAY
1 2 3 4 5
DAY
1 2 3 4
DAY
31.5
31.0
30.5
30.0
29.5
29.0
ESTIMATED ACCLIMATION TEMPERATURE, °C

Water temperatures at fish-collecting sites ranged from 25 to 36 C. Thus, YOY bluegills at different locations in the outfall area were acclimated to temperatures comprising a narrow interval in the range of available habitat temperatures. Moreover, individual fish within each location were apparently acclimated to virtually the same temperature, because variation of resistance times within samples of fish from the outfall area did not differ greatly from variation within samples of laboratory acclimated fish having corresponding median resistance times.

Although all samples of bluegills from the outfall area had estimated acclimation temperatures within a 1.9 C interval the four locations nevertheless yielded differently acclimated fish. The difference in acclimation between fish from either side of each jet implied that YOY bluegills did not freely mingle across the jets, particularly the primary jet. The continuous, high velocity discharge from the primary outfall probably constituted a more effective barrier to along-shore movements of young bluegills than did the intermittent, diffuse flow from the secondary outfall.

PART II

BEHAVIORAL REGULATION OF TEMPERATURE BY FISHES IN THE LABORATORY

Introduction

To evaluate the extent to which temperature might govern distributions of fishes in the outfall area of Lake Monona, thermoregulatory behavior of representative species was investigated in the laboratory.

Temperatures preferred by fishes were determined by allowing specimens to behaviorally regulate the temperatures of tanks in which they lived. Temperature preference data were collected from young fish representing six species that differed among themselves in the temperatures at which they occurred during summer in the outfall area.

Additional experiments with two of the six species explored the behavior of fish in environments with food available at one of two temperatures but not at the other. The object of these experiments was to determine whether fish might invade water warmer or cooler than the preferred temperature to get food.

General equipment and procedures

Test Tanks

Each of ten test tanks was a 50-liter fiberglas aquarium with one glass side; inside dimensions were 60 cm by 30 cm by 30 cm deep.

A double-walled partition of black (opague) plexiglas divided each tank into halves. A tube (40 mm inside diameter) of black polyethylene penetrated the center of the partition to form a 6 cm long tunnel through which a fish could swim from one half of the tank into the other (Figure 10).

An electronic monitoring system (Figure 10) sensed and recorded the time and direction of each pass of a fish through a tunnel. Sensing elements of each test unit were a pair of photocells in waterproof glass tubes. The photocells received light passing horizontally across the tunnel from a pair of light sources (red, about 6500 Å) mounted in tubes which penetrated the tunnel's opposite wall. Even partial interruption of a light beam by a fish caused electrical resistance of the receiving photocell to increase. The resulting voltage drop through the photoelectric cell, amplified by transistors, produced a change in state of a bistable multivibrator, the output of which was recorded on one channel of a 20-channel event recorder. State of the multivibrator and, thus, the signal to the recorder were determined by which light beam (right or left member of the pair) was last interrupted. Whether a fish passed completely through the tunnel or only entered the tunnel to then back out into the same side of the tank, the result of the action was correctly interpreted: After the move, the fish was in that half the tank adjacent to the light beam last broken. A second channel of the event recorder was activated whenever either or both light beams

were blocked, whether or not a change occurred in state of the multivibrator. The two channels together provided a continuous, unambiguous, and permanent record of a single fish's movements between the halves of each tank through time.

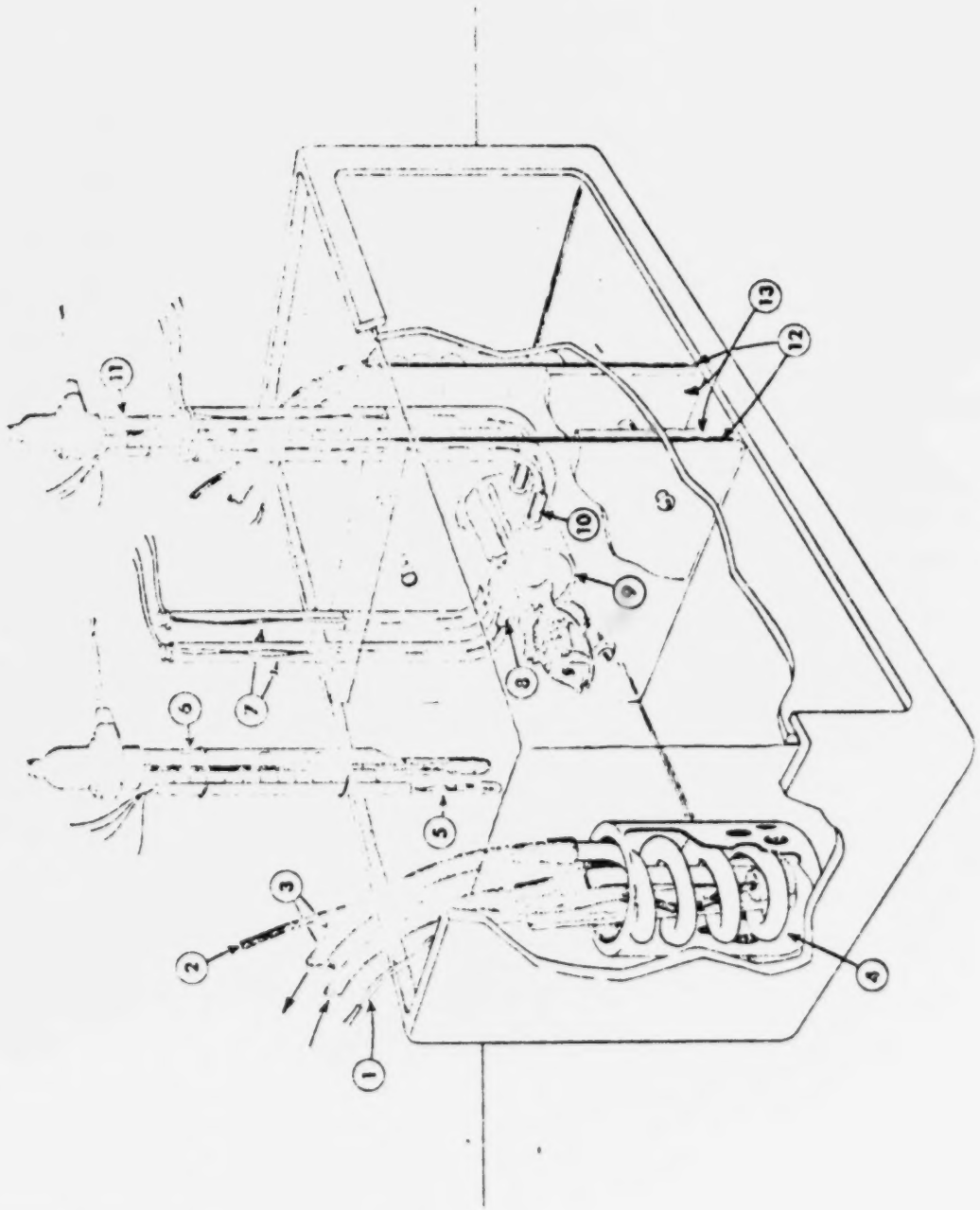
Each half of each test tank was supplied with the following basic equipment (Figure 10):

1. a compressed air diffuser for aerating and mixing the water;
2. one or more submersible aquarium heaters switched by a mercury contact thermometer through a solid state relay to precisely maintain above-ambient temperatures;
3. a coil of acrylic-coated copper tubing through which cold water could circulate to decrease ambient temperature;
4. a 0.5 liter polyethylene bottle (with holes, and the top half removed) which contained the cooling coil, heaters and air diffuser--an arrangement which increased the efficiency and precision of temperature control;
5. a truncated tetrahedron of clear, 3 mm thick plexiglas panes that formed a "funnel," the smaller end of which surrounded the mouth of the tunnel to facilitate location of the tunnel by the fish, especially during darkness; and
6. a 0.5 liter glass jar covered with black polethylene film and laid on its side at the bottom of the tank to provide cover for the fish.

Figure 10 Diagram of test tank.

1. cord to heater
2. compressed-air line to air diffuser
3. supply and return lines (Tygon) for cooling coil
4. cooling coil
5. glass tube containing thermistors (from temperature recorder and comparator)
6 and 11. contact mercury thermometer
7. glass tubes[1] containing photocells
8. photocell
9. tunnel
10. light source
12. walls (opague plexiglas) of partition
13. styrofoam for insulation

[1]glass tubes containing both photocells and light sources were wrapped with black vinyl tape to exclude extraneous light.


13
12
11
10
9
8
7
6
5
4
3
2
1

Holding Tanks

Except during tests, experimental fishes lived in 30 to 200 liter holding tanks. Submersible heaters switched by contact thermometers through solid state relays enabled precise (±0.1 C) control of temperature in some holding tanks. Other tanks had no temperature control equipment and fluctuated with ambient temperature (18-23 C). Cooling coils were not used in holding tanks.

Illumination and Photoperiod

The test and holding tanks were in an enclosure covered with black polyethylene film to exclude extraneous light (and other visual information). Each test and holding tank was illuminated by an incandescent bulb centered 15 cm above the water. The test tanks and 30 and 50 liter holding tanks were lighted by 15 w bulbs; a 25 w bulb lighted the single 200 liter holding tank. Illumination was controlled by capacitor-dimmer circuitry coupled to a 24-hr timer to provide a 14:10 photoperiod (the 1 August photoperiod at Madison). The diel cycle of light consisted of four phases:

1. 0600-0700 CST: "dawn," during which the lamp above each tank went from off to maximum brightness;
2. 0700-2000: "day," during which the lamps were at maximum brightness;
3. 2000-2100: "dusk," during which the lamps went from maximum brightness to off; and

4. 2100-0600: "night," during which the lamps were off. If we had to enter the enclosure at night, a flashlight provided dim, red light.

Water

Only filtered (otherwise untreated) Lake Mendota water was used in all tanks. Water in each tank was continuously aerated. Some water from each tank was exchanged for fresh water at least once every week for holding tanks, or once every three days for test tanks.

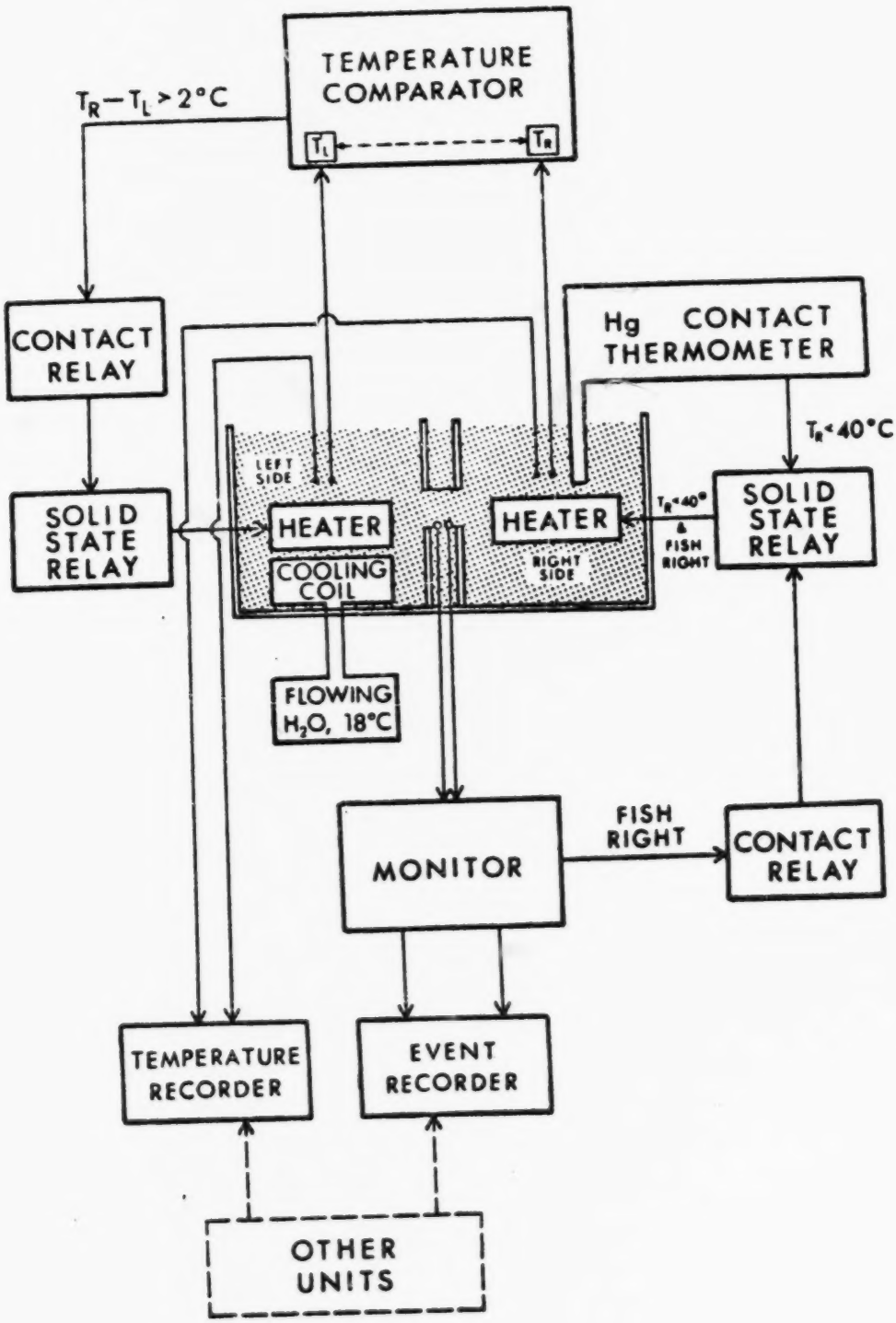
Maintenance of environmental temperature by behavioral thermoregulation

Experimental Technique and Procedures

Eight of the ten test tanks were modified to evaluate thermoregulatory performances of young fishes (Figure 11).

The left-right signal from the monitor unit of each tank was used to activate a contact relay wired in parallel with the left-right relay of the event recorder. The extra relay switched on the heater(s) in one side (randomly selected) of the tank whenever the test fish moved through the tunnel into that side. The heaters continued to operate until either 1) fish swam back through the tunnel to the other side (cooler side) of the tank, or 2) temperature of the warmer side increased to the level set by the mercury contact thermometer, which caused automatic cutoff. As temperature of the warmer side increased or decreased (within the range, 20-40 C), the other side remained at every instant 2.0 ± 0.3 C cooler through the action of a comparator relay (Magsense Comparator, Model 82T).

Figure 11 Schematic diagram of the experimental system for behavioral thermoregulation. (see text for details of operation).


TEMPERATURE COMPARATOR
$T_R - T_L > 2°C$
T_L
T_R
CONTACT RELAY
Hg CONTACT THERMOMETER
$T_R < 40°C$
LEFT SIDE
SOLID STATE RELAY
HEATER
COOLING COIL
HEATER
RIGHT SIDE
$T_R < 40°$ & FISH RIGHT
SOLID STATE RELAY
FLOWING H_2O, 18°C
MONITOR
FISH RIGHT
CONTACT RELAY
TEMPERATURE RECORDER
EVENT RECORDER
OTHER UNITS

The comparator interpreted the difference in electrical resistance between two thermistors (temperature-sensitive resistors), one in either half of the tank; the heaters on the cooler side were switched on or off by the comparator to maintain the 2 C differential. Water at 16-18 C, continuously circulated through the coil in the cooler side, caused the rate of heat loss from the cooler side to exceed that from the warmer side. Excess heat removal from the cooler side served 1) to maintain a rate of cooling (when the fish was in the cooler side) approximately equal to the rate of warming (when the fish was in the warmer side)--3 to 5 C/hr; and 2) to preserve the 2 C differential at tank temperatures below room temperature.

A fish in a test tank could regulate its thermal environment by exercising temperature selection behavior. The fish need only spend most of its time in that half the tank with the preferable temperature, changing sides whenever rising or falling tank temperature reversed the relative value of the two sides.

Most young fishes placed in the tanks learned to swim through the tunnel within a few hours. During a training period of three to seven days, both sides of each test tank fluctuated with ambient temperature (20-22 C), or maximum attainable temperature of the warmer side was limited to 22 C by contact thermometer. On the last day of training, maximum

attainable temperature of the warmer side was advanced to 30 C and then, 24 hrs later, to 40 C. During all experiments, temperature of each side of each test tank was recorded from a thermistor once every six minutes by a multi-channel analog recorder.

Species tested were carp, rock bass, bluegill, largemouth bass, black crappie, and yellow perch. Young carp were seined in October 1969 from a small oxbow of the Wisconsin River, 20 km below Prairie de Sac-Sauk City, Wisconsin. Black crappies and largemouth bass were seined from Lake Mendota on 21 April and 23 August, respectively, 1970. All other specimens were caught by seine or push-net from Lake Monona between 15 August and 15 September 1970. All specimens were less than one year old when they were collected.

Thermoregulatory tests began on 6 August 1970 and ended 20 November 1970. Largemouth bass entered the test tanks the day after capture. All other specimens lived in the holding tanks at ambient temperature (20-22 C) for at least 15 days prior to tests. Carp and black crappies, both kept under uncontrolled light conditions for several months after capture lived in the experimental light environment for more than 30 days before they were tested. Total lengths of specimens at the end of tests were carp, 81-97 mm; rock bass, 48-59 mm; bluegills, 53-83 mm; largemouth bass, 65-75 mm; black crappies, 75-88 mm; and yellow perch, 82-118 mm. The numbers of fish tested were 5 carp, 6 rock bass, 13 bluegills, 8 largemouth bass, 8 black crappies, and 17 yellow perch.

Fishes were fed once daily during holding and training and twice daily during thermoregulatory tests. Food was put into that side of each test tank in which the fish occurred at the moment of feeding.

Results

Regulatory performance varied with species, individual specimen, and time of day. Individual bluegills were the best regulators, yellow perch poorest, and the others intermediate. Upper and lower turn-around temperatures during the three-day trials are presented in Figure 12 for the first specimen tested of each species. These records exemplify the performance of each species but are representative only in that they were selected without regard for their specific content. The specimen which kept its environmental temperature most nearly constant was a bluegill; this fish, on the first day of the trial, kept the warmer side of the tank between 31.5 and 32.0 C from 0600 to 1400, between 31.7 and 33.0 C from 1400 to 1700, and between 32.2 and 32.5 C from 1700 to 2000.

Each species maintained environmental temperature between limits different from those observed by one or more of the other five species (Figure 13). Carp and bluegills maintained temperatures between 28.5 and 33.5 C. Largemouth bass regulated at temperatures lower than carp and bluegills but somewhat higher than rock bass and black crappies, both of which avoided temperatures lower than 25.5 C or higher than 30.0 C. Yellow perch avoided temperatures higher than 26.5 C; they kept their environment decidedly cooler than did any other species.

Figure 12 Upper (∧) and lower (V) turn-around temperatures during a three-day trial for the first carp, bluegill, largemouth bass, black crappies, rock bass, and yellow perch tested in experiments on maintenance of environmental temperature by behavioral thermoregulation.

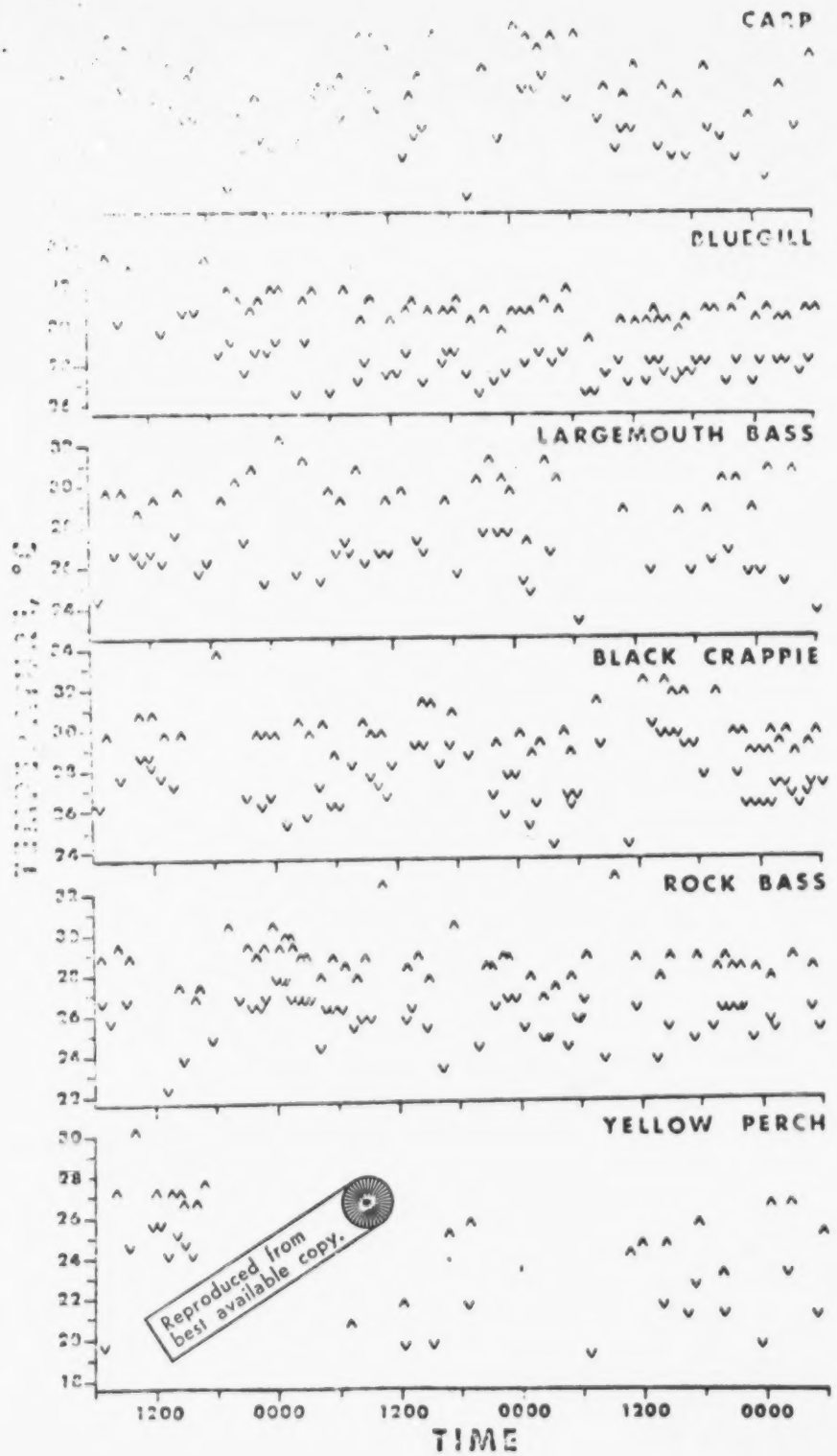


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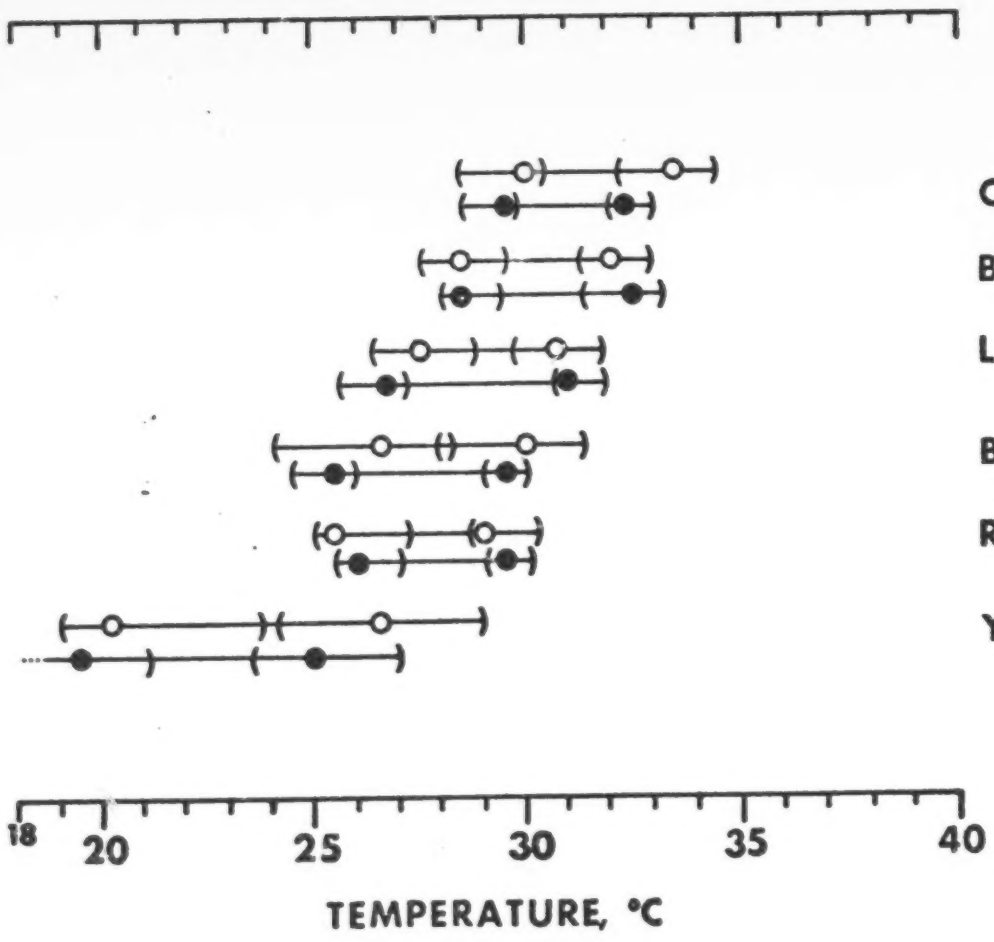
Figure 13 Medians and interquartile ranges of upper and lower turn-around temperatures for thermoregulating carp, bluegills, largemouth bass, black crappies, rock bass, and yellow perch. Medians during day and night are indicated by open and solid circles, respectively. Parentheses about medians indicate the interquartile range of turn-around temperature. The number of fish tested is given in parentheses to the right of each species' name. (See text for definition of turn-around temperatures.)


CARP (5)
BLUEGILL (13)
LARGEMOUTH BASS (8)
BLACK CRAPPIE (8)
ROCK BASS (6)
YELLOW PERCH (17)
18
20
25
30
35
40
TEMPERATURE, °C

Whether or not yellow perch entered into the analysis, the species differed significantly among themselves in both upper and lower limits within which they maintained environmental temperature (Kruskal-Wallis one-way AOV; $< p\ 0.01$).

A preferred temperature range could be defined for each species: the region of temperature bounded by the median upper and lower turn-around temperatures. The preferred temperature range for perch was about 6 C wide. For the other five species, it was a most constant in width--about 3.5 C.

For no species was there a significant difference between day and night medians of either upper or lower turn-around temperature. However, the variation among regulatory performances individuals did change from day to night; in each species; upper as well as lower turn-around temperatures were less variable at night than during the day (Figure 13).

Discussion

Activity level and thermoregulatory performance were not independent of each other. More active fish, for example bluegills, kept their environment warmer than did less active fish like yellow perch. Whether activity and thermoregulation were related as cause and effect could not be determined.

In these experiments, width of the preferred temperature range for each fish could never be less than 2 C, the differential between the two sides of the tank. A differential of 2 C was chosen for several reasons. In preliminary experiments in which the sides of a tank were set at constant temperatures 1 C or

2 C apart, selection of one side over the other by bluegills and black crappies was more consistent when the difference was 2 C. A 2 C differential was also more compatible with intrinsic comparator limitations than were smaller or larger differentials. Finally, larger differentials were difficult to manage because of heat flux problems.

Turn-around temperatures were probably species-specific and independent of initial acclimation temperature. Before tests, each fish (except largemouth bass) was held at temperatures between 20 and 23 C; yet, turn-around temperatures varied greatly among species. Acclimation probably increased rapidly during the two days preceding data collection. Within a few hours after we relinquished control of maximum tank temperature, most fish raised their environmental temperatures to the level maintained for the duration of the experiment. There was no indication of consistent drift in thermoregulation toward either higher or lower temperatures during the trials.

Thermoregulatory performances of our fish were generally consistent with available information on their final temperature preferenda. The final temperature preferendum (Fry, 1947) is the temperature about which fish living in a temperature gradient will ultimately congregate, regardless of their previous thermal experience. Fry and others (see Fry, 1964) have considered the final preferendum to be species-specific. Published data are available for two of the six species; carp and yellow perch have final preferenda of 32.0 C (Pitt, Garside, and Hepburn, 1956)

and 24.2 C (Ferguson, 1958), respectively. Ferguson (1958) cited unpublished, manuscript values for bluegills and largemouth bass. These are 32.3 C for bluegills and 30-32 C for largemouth bass. All four species have final temperature preferenda somewhat nearer the upper than lower turn-around temperatures we recorded. This difference in turn-around temperatures relative to the final preferendum was not unexpected because fishes typically prefer temperatures much nearer the upper than lower lethal levels (see data compiled by Fry, 1964).

Behavioral thermoregulation in fishes has been investigated most often by observing the distribution of specimens in temperature gradients. Fry (1964) and Ferguson (1958) have reviewed the methods and results of several of these studies, the object of which has been estimation of final temperature preferenda. In the approach suggested by Fry (1947) and followed by several scientists at the University of Toronto and elsewhere, temperatures preferred by differently acclimated fish are measured and plotted against acclimation temperatures. Ordinarily, preferred temperature increases as acclimation temperature increases; but, fish acclimated to some low temperature prefer a temperature exceeding acclimation temperature, whereas fish acclimated to some higher temperature prefer a temperature below the acclimation temperature. The point at which preferred and acclimation temperatures are the same is considered by Fry (1947) to represent the final temperature preferendum. A more direct but more time-consuming measure of final temperature preferenda was used by Bacon, Neill, and Kilambi (1968) and Alabaster and

Downing (1966). These workers simply kept fish in large gradient tanks for several weeks until effects of initial acclimation subsided, and the fish adopted a persistent distribution about the final preferendum.

A quite different technique for studying thermoregulatory behavior in fishes was advanced by Rozin and Mayer (1961). Young goldfish were trained to press a lever which caused a small transitory decrease in the temperature of their tank.

Our technique for measuring temperature preference was unique in several respects. Fish could regulate both limits of temperature by doing no more than they must do in nature: move a short distance from less to more desirable locations within the thermal environment. Difficulties of maintaining stable temperature gradients were avoided because only two different temperatures were required at any instant. The use of two compartments (instead of many) and continual reversals of their relative thermal preference values minimized the tendency for fish to form spatial preferences which can (Neill, 1967) interfere with thermoregulatory behavior. Automated operation of the apparatus allowed continuous, remote acquisition of data, even at night; potential effects of a human observer on fishes' behavior were largely eliminated.

Effect of food availability on behavioral thermoregulation

Implementation of Automated System for Delivery of Food

The ten test tanks were modified so that fish gained access to food by spending time in one half of a tank but not in the other.

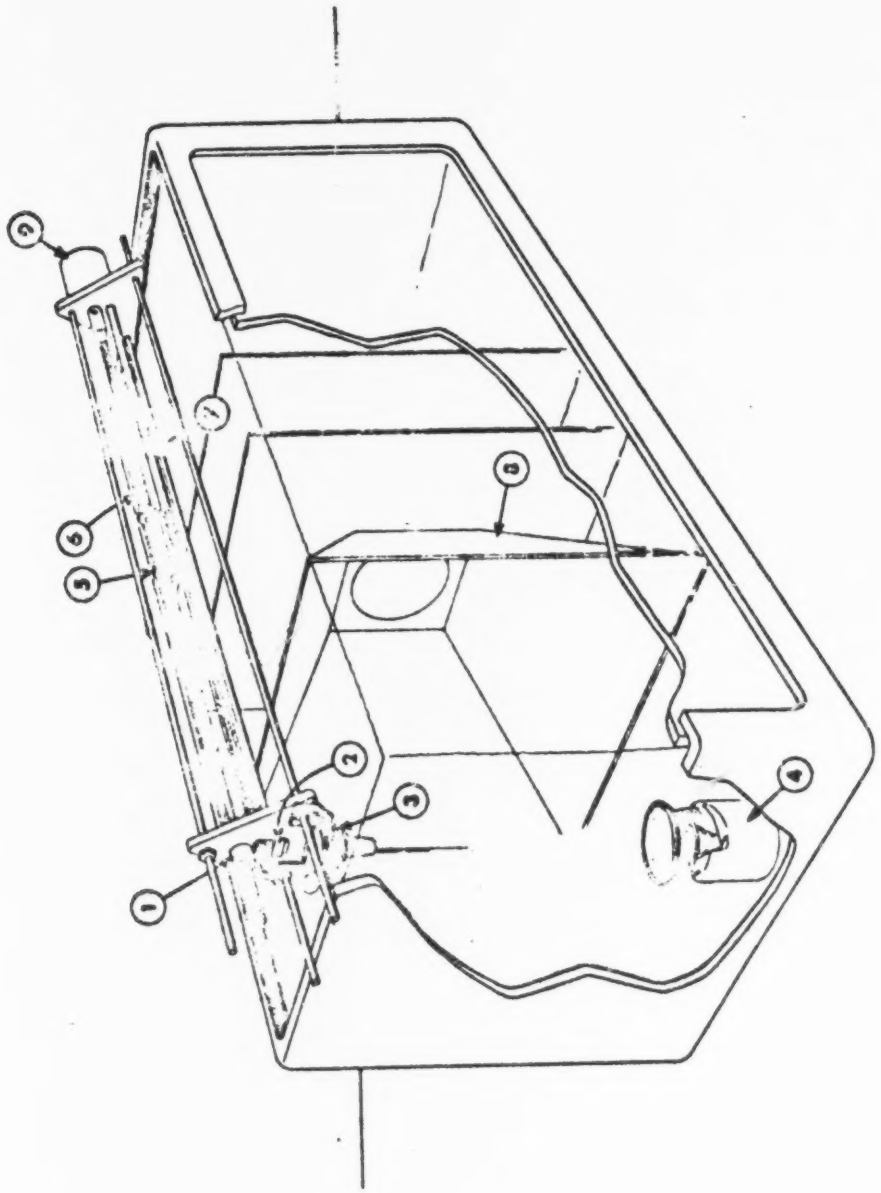
Each test tank was equipped with an automatic pellet dispenser, or feeder (Figure 14). The glass tube served as a magazine for food pellets, each about 3 mm long and 3 mm in diameter. The motor turned a worm gear made from the threaded rod. The larger magnet made contact with the magazine's outer wall and moved along the magazine as the worm gear rotated. Food was pushed out the open end of the magazine, one pellet at a time, by the smaller magnet as it was moved along by the larger magnet.

The feeders dispensed food into one half (food side) of each tank about 25 cm from the tunnel mouth (Figure 14). Each pellet fell into a small funnel, the tip of which was 3 cm beneath the surface of the water. When the pellet was wetted sufficiently to sink, it passed through the funnel tip and, unless intercepted by the fish, fell into a second small funnel. The latter funnel formed a throat into a 0.2 liter glass jar on the floor of the tank. Each pellet was available to the fish for about 2 sec while it sank through 15 cm of water between the funnels. Pellets not intercepted accumulated in the glass jar.

Each feeder was activated only while the fish was in the food side of its tank between 0700 and 1830 CST. A timer triggered a switch to supply power to all feeders potentially between 0700 and 1830. However, each feeder was activated during this 11.5 hr interval only while the fish was in the food side of

Figure 14 Diagrams of an automatic food dispenser installed on a test tank. (See text for details of operation and specifications not presented below.)

1. brass sleeve to permit free rotation of worm gear
2. latch to secure pellet magazine in feeder
3. upper funnel
4. jar with funnel to collect unintercepted pellets
5. magnet assembly
6. worm gear (threaded brass rod)
7. pellet magazine (glass tube)
8. funnel (for guiding fish to mouth of tunnel)
9. motor


6
1
8
6
5
2
3
4
1

the tank, the monitoring system only then closing the contacts of a relay to complete the circuit to the feeder motor.

Each test fish, then, had access to approximately one pellet for every 5 min spent in the food side of its tank during 11.5 hrs each day. Because the magnets of each feeder traveled 38.1 mm for every hour the fish spent in the food side of its tank, total time in the food side during each day's feeding period was easily determined by measuring distance traveled by the magnets.

Experimental Procedures

Three experiments were performed. In each experiment, temperature in the right side of each tank was the midpoint of the preferred range (T_p) determined from thermoregulatory tests described above. The left side of each tank was also maintained at Tp for four days; thereafter, the left side was either cooler or warmer than the right side.

In the first experiment, fish were offered food at temperatures above or below Tp (food side = left side). One fish acclimated to Tp was put into each test tank, both sides of which were maintained by contact thermometer at Tp for four days. During this period, the fish received only food dispensed by the feeder into the left side of the tank. After the last day of the training period, between 1830 and 2000, temperature of the left side was increased 2 C in five tanks and decreased 2 C in the other five tanks. The right side of all tanks remained at Tp. Thereafter, left-side temperature was progressively increased or decreased 2 C between 1830 and 2000 on each successive day.

The second experiment repeated the first, except that the feeders dispensed food into the right side of each tank (food side = right side). Thus, food was available at temperature Tp between 0700 and 1830 each day but never at temperatures above or below Tp.

A final experiment allowed fish to choose on several consecutive days between Tp without food and a single temperature above Tp with food; the object of this experiment was to determine if the fraction of time fish spent in the food side might change after the first day. One fish was put into each of five test tanks, both sides at Tp, with food dispensed on the left side (food side = left side). At the end of the training period temperature of the left side was increased to Tp+4C (bluegill) or Tp+6C (yellow perch). This regime was then maintained six days with no further changes in temperature.

Bluegills (63-93 mm long) and yellow perch (105-129 mm long) were used in these experiments because of their divergent preferred range midpoints--30 and 23 C, respectively.

Experiment 1. Food Available at Non-preferred Temperatures (in Left Side of Tank)

When both sides of all tanks were at temperature Tp (final day of training), bluegills and yellow perch spent about 73% and 43%, respectively, of the feeding period in the left side of their tanks (Figures 15 and 16). Then, as temperature of the left side increased or decreased, both species reduced the percentage of time spent in the left side (PTL) as the difference between temperatures of left and right sides increased. Median

Figure 15 Medians and interquartile ranges of time spent at various temperatures in the left side of tanks by bluegills fed in the left side and by bluegills fed in the right side when, in each case, the right side was at the preferred temperature (Tp), 30 C. Medians for bluegills fed in left and right sides are indicated by solid and open circles, respectively; vertical lines about medians indicate interquartile ranges for samples of three to five fish.

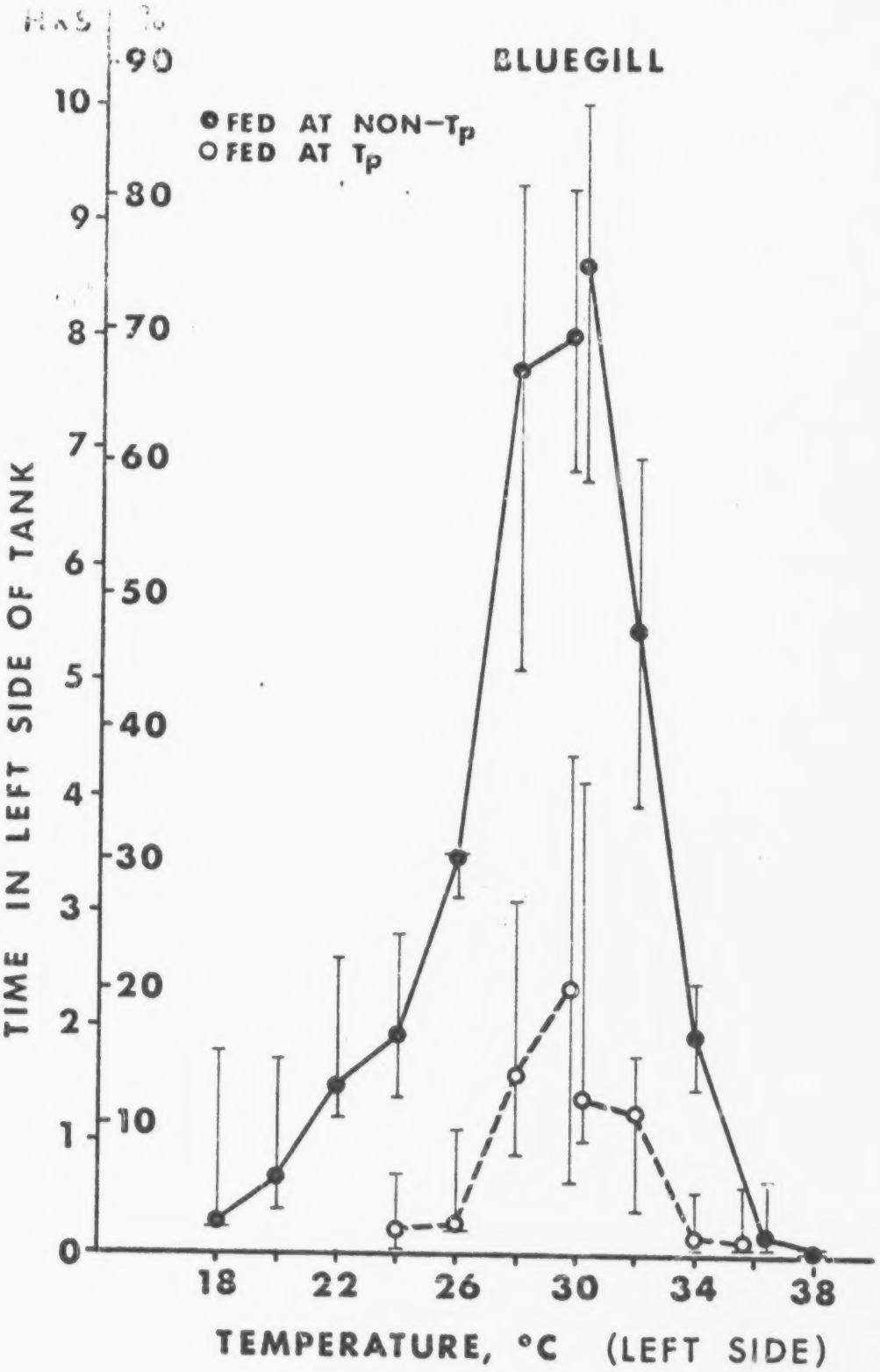
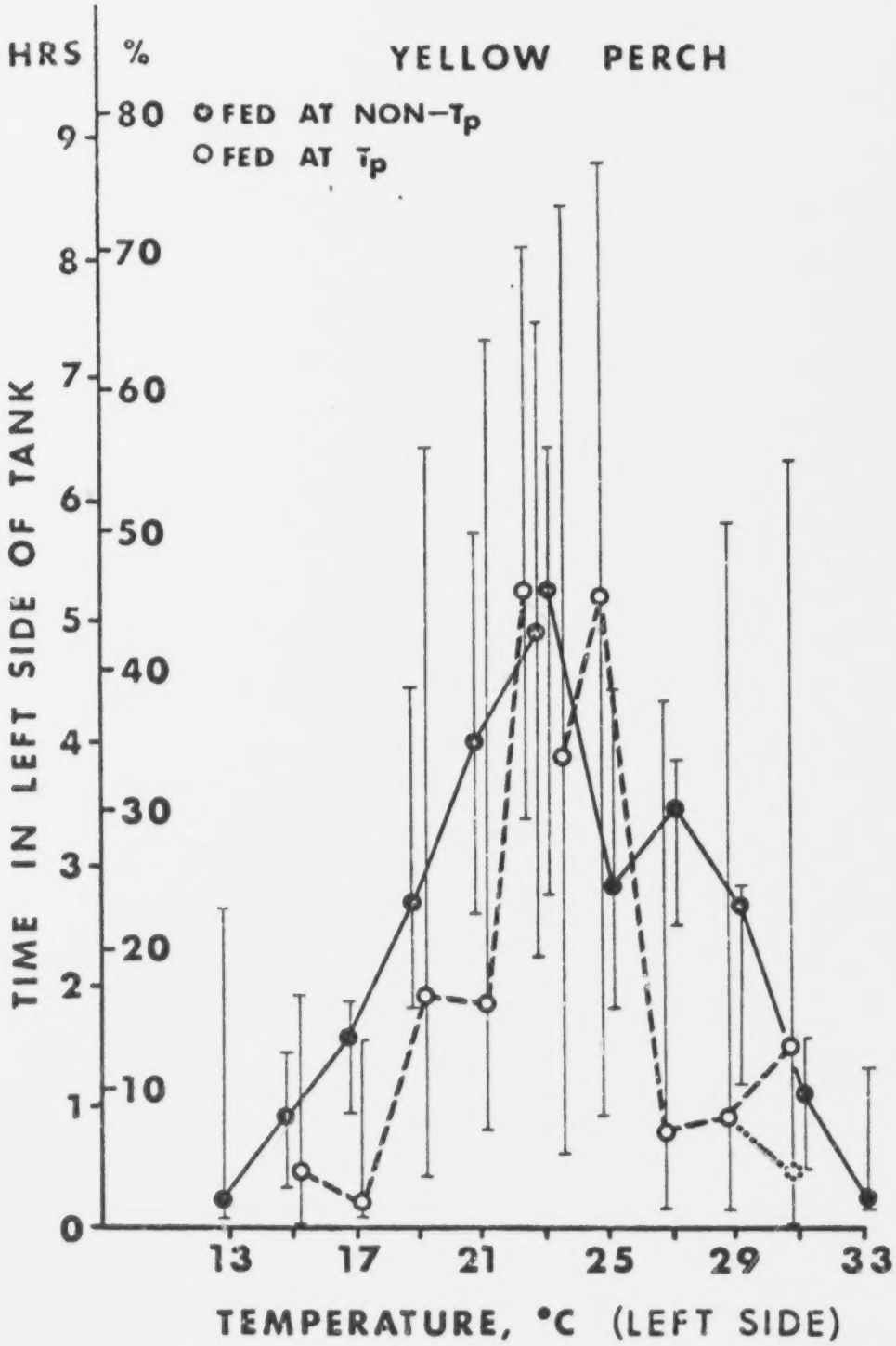

BLUEGILL
FED AT NON-T_p
FED AT T_p
TIME IN LEFT SIDE OF TANK
TEMPERATURE, °C (LEFT SIDE)
0
1
2
3
4
5
6
7
8
9
10
10
20
30
40
50
60
70
80
90
18
22
26
30
34
38

Figure 16 Medians and interquartile ranges of time spent at various temperatures in the left side of tanks by yellow perch fed in the left side and by yellow perch fed in the right side when, in each case, the right side was at the preferred temperature (Tp) 23 C. Medians for perch fed in left and right sides are indicated by solid and open circles, respectively; vertical lines about medians indicate interquartile ranges for samples of four or five fish. (See text for explanation of dotted open circle).


HRS
%
YELLOW PERCH
FED AT NON–Tp
FED AT Tp
TIME IN LEFT SIDE OF TANK
0
1
2
3
4
5
6
7
8
9
10
20
30
40
50
60
70
80
13
17
21
25
29
33
TEMPERATURE, °C (LEFT SIDE)

PTL of bluegills dropped to 50% of the initial level at about 26 and 33 C and to 5% at about 20 and 35 C (by interpolation, Figure 15). Thus, decrease in PTL for bluegills was somewhat more steep as left-side temperature increased than as it decreased. For perch, decrease in PTL was more symmetric about Tp and less abrupt than for bluegills. Fifty per cent reduction occurred at about 19 and 29 C and 95% at about 14 and 33 C (by interpolation, Figure 16). PTL was more variable among individual perch than among individual bluegills.

Experiment 2. Food Available at the Preferred Temperature (in Right Side of Tank)

When both sides of each tank were at temperature Tp, bluegills and yellow perch spent about 16% and 40%, respectively, of the feeding period in the left side of their tanks (Figure 15 and 16). If allocation of time under initial temperature conditions in this experiment was the same as in the first, bluegills spent 73% of the feeding period in the side with food and 16% in the side without food whereas perch spent almost equal time in the sides with and without food--43% and 40%, respectively. The remainder, 11% for bluegills and 17% for perch, could be attributed to time the fish spent resting in the tunnels; these percentages were consistent with tunnel time estimated from the event-chart records.

As in the first experiment, PTL decreased as left-side temperature decreased or increased from T_p (Figures 15 & 16). As left-side temperature diverged from T_p, PTL of bluegills remained dramatically below those during the first experiment. Although

the difference between experiments was less marked with perch than with bluegills, median PTL of perch at temperatures above and below Tp were also significantly lower during this experiment than in the first (one-tailed Wilcoxin test; p=0.05).

Perch were generally more variable in their responses during this experiment than in the first, and medians of PTL fluctuated about the trend relating PTL to temperature (Figure 16). Among perch in tanks with increasing left-side temperature was one fish that consistently spent more than 75% of its time in the wramer side. The aberrant response of this fish affected median PTL most on the final day of the experiment (left side 31 C); on that day, another fish had to be excluded from analysis because the right side of its tank was potentially 3 C too warm during the first 3.5 hrs of the feeding period. If data from the excluded fish were considered acceptable, median PTL at 31 C was reduced from 13% to 4% of total time (dotted circle, Figure 16).

In neither species was there a substantial change during this experiment as compared with the first in the rate at which PTL decreased as left-side temperature diverged from T_p (Figure 15 and 16). However, bluegills and yellow perch did spend more time at non-preferred temperatures when food was available only at those temperatures than when food was available only at the preferred temperature. When fed at the preferred temperatures, bluegills and perch spent less than 5% of their time at temperatures outside the ranges 26-34 C and 17-31(?) C, respectively.

These ranges increased in width to 18-36 C for bluegills and 13-33 C for perch when food was not available at preferred temperatures.

Initial differences in foray behavior during the second experiment did not result in substantially different distributions of total time between tank halves. PTL did not differ significantly among experimental groups under initial temperature conditions in either of the two experiments with either species. Similar allocations of total time were possible despite differences in foray behavior because an inverse relationship existed between foray frequency and duration. Thus, two fish under identical conditions of temperature and food distribution tended to accumulate similar amounts of time on the left side of the tank even though one made many short forays whereas the other made fewer but longer forays.

Experiment 3. Food Available for Six Consecutive Days at a Non-preferred Temperature (in Left Side of Tank)

PTL under initial temperature conditions did not differ significantly from those observed in the first experiment Median PTL were 76% for bluegills and 41% for yellow perch. On the second day after left-side temperature was increased to 34 C for bluegills and 29 C for perch, PTL decreased to levels similar to those observed at the same temperatures in the first experiment. Median PTL of neither species changed significantly during the remainder of the experiment. However, variability of PTL among perch may have increased toward the

end of the experiment.

Lack of change in PTL during the final five days of the experiment suggested that all potential adjustment to temperature heterogeneity may have been effected by the second day after left-side temperature was raised from T_p. Although temperature--acclimation levels of fish at the end of the experiment must have been higher than at the beginning, the data did not offer evidence for or against dependency of PTL on acclimation level. If PTL did depend on level of temperature acclimation, complete acclimation to 34 C in bluegills and 29 C in perch may have occurred during the first day after these temperatures became available.

Discussion

Bluegills and yellow perch responded similarly when allowed to partition their time in an environment of two parts--one with temperature T_p and the other with a temperature which increased or decreased from T_p at 2 C/day. Each species decreased the proportion of time spent at the alternative temperature as it diverged from T_p. This response occurred whether food was available at T_p or at the alternative temperature.

However, a larger proportion of time was spent at any alternative temperature when food was available only at the temperature than when food was available only at T_p. Conversely, temperatures of the alternative environment diverged farther from T_p before fish which were fed there reduced occupancy to the same proportion of time as fish fed at T_p. Bluegills were excluded more

than 95 % of the time from the side of a tank without food when its temperature decreased to 26 C or increased to 34 C but, with food, only when temperature decreased to 18 C or increased to 36 C. Yellow perch were similarly excluded at 17 C and 31 C from alternative environments lacking food but only at 13 C and 33 C from those with food. Thus, alternative temperatures at which bluegills and perch spent at least 5% of the feeding period spanned 8 C and 14 C when food was available at T_p but 18 and 20 C when food was available at the alternative temperatures.

Although availability of food clearly biased the distribution of each species at extreme temperatures, only bluegills elected to spend a disproportionately large fraction of time in the compartment with food when both halves of the tank were at temperature T_p. The time so spent--about 70% of the feeding period--was much more than necessary to keep the stomach filled with food, even if the efficiency of pellet interception was only 50%. (Bluegills fasted for 24 hrs were observed to intercept and eat as many as 12 consecutively dispensed pellets; so the efficiency of "hungry" fish may have been considerably greater than 50%). A fish of median weight (10 g bluegill; 12 g perch) gained potential access to its maximum daily meal by spending only about 15% of the feeding period in that half of the tank with food.

Temperature did eventually limit each species' acquisition of a maximum daily meal. Bluegills did not obtain a maximum

daily meal at temperatures below 24 C or above 34 C; temperatures limiting acquisition of maximum daily meal for perch were 17 C and about 30 C.

Acclimation of fishes to an increase in temperature occurs much more rapidly than acclimation to a decrease of equal magnitude (Brett, 1944 and 1946; Heath, 1963; Loeb and Wasteneys, 1912). Moreover, upward acclimation over a temperature interval of given length proceeds more rapidly the higher the end-point temperature (Brett, 1946). Therefore, acclimation levels of fish which experienced increasing temperatures in these experiments may have kept pace with the 2 C/day temperature rise. In contrast, acclimation levels of fish in tanks with decreasing temperature probably remained near T_p throughout the experiments because the time spent at low temperatures was unlikely to have been sufficient for much downward acclimation.

If acclimation states were as supposed, thermal stresses governing time spent in food environments with increasing and decreasing temperature were of different types. Time spent at temperatures increasing from T_p became much reduced as those temperatures approached the ultimate upper lethal limits, 35 C for bluegills and 32 C for yellow perch (Fry, 1964); above these temperatures, each species spent less than 5% of time. But, both bluegills and perch curtailed time to less than 5% when decreasing temperatures were still several degrees above the lower lethals for T_p acclimated fish--about 12 C for bluegills (Hart, 1952) and probably less than 4 C for perch (Fry, 1964). Thus,

bluegills and perch were practically excluded from environments with food when temperatures exceeded the ultimate upper lethals or when temperature dropped about 10 C below the acclimation temperature, T_p. In the case of increasing temperature, exclusion was apparently caused by the fishes' absolute inability to acclimate to temperatures above the lethal limits. At decreasing temperatures, however, the limits were apparently set by fishes' unwillingness to endure non-lethal stresses imposed by temperatures several degrees below the acclimation levels.

Although neither species spent much time at temperatures above the upper lethal limits, the median bluegill and perch that were fed at increasing temperatures did make about 20 and 40 forays, respectively, into water 3 C above the upper lethal temperature. These fishes would have died within a few hours had passage back into the T_p environment been prevented during a foray. Perhaps, the two perch that died at 35 C during the first experiment were prevented from returning to 23 C by their decreased ability, in darkness, to find the tunnel.

Midpoint of the preferred temperature range, 30 C for bluegills and 23 C for yellow perch, was confirmed as a reasonably accurate estimate of the preferred temperature. Had a temperature 2 C above or below T_p been preferred over T_p, the fraction of time spent in the alternative environment at that temperature should have increased over that when both environments were at T_p. No substantial increase was observed in any of the experiments. That is, relative to an environment at T_p but without food, no combination of temperature and food was preferred over

T_p with food. Also, relative to an environment at T_p with food, no temperature without food was preferred over T_p without food.

Only bluegills spent more time at some temperature if food was offered there than at T_p without food. If 11% of each feeding period was spent in the tunnel, then the fraction of time spent in the compartment with food was not reduced to equal that spent at T_p without food (44.5%) until the temperature of the food compartment decreased to about 27 C or increased to 32 C. In this sense, the environment preferred by bluegills was shifted 3 C downward and 2 C upward from the preferred temperature by the availability of food in that environment when no food was available at the preferred temperature.

INTEGRATION AND CONCLUSIONS

Distribution of Lake Monona fishes relative to the outfall area

Lake Monona fishes were diversely distributed within the littoral zone. Some fishes regularly avoided the outfall area; these were yellow perch, mottled sculpin, subadult yellow bass, and subadult black bullheads. Others were occasionally or usually concentrated in the outfall area relative to reference areas--longnose gar, large carp, large yellow bass, young rock bass, young pumpkinseeds, bluegills, and largemouth bass. Still other fishes, even though some were caught in relatively large numbers could not be placed with conviction in either group. Among these were subadult carp, large pumpkinseeds, black crappies, Iowa darters, and log perch. Thus, distributions varied not only among species but also among size classes within some species.

Distributions of fishes also differed among seasons and, within seasons, between day and night. Kinds sizes, and numbers of fish fluctuated throughout the littoral zone. However, the abundance of most fishes in the outfall area approximated a constant ordinal relationship to their abundances in reference areas from season to season and from day to night. Although several fishes (e.g., yellow bass, bluegill, largemouth bass) tended to be more uniformly distributed at night than during the afternoon, no size class of a species was significantly more abundant in one area during the afternoon but in another at night. In only two cases were there significant seasonal reversals in the ordinal relationship between areas. Small bluegills were more abundant

in the reference areas during November 1968 but in the outfall area during most other seasons. Small black crappies were more abundant in the outfall area during summer 1968 but in the reference areas during summer 1969.

Fish distribution, temperature, and behavioral thermoregulation

Results of the different research phases argued jointly that the varied distributions of fishes among outfall and reference areas during summer reflected primarily different behavioral responses to temperature. The lines of evidence supporting this conclusion are listed and discussed below.

1. During summer, fishes in the outfall area were generally not uniformly distributed with respect to temperature, and different fishes tended to be most abundant within different ranges of available temperature.

Catch/effort from 50 m transects indicated that fishes were not equally abundant at all temperatures and that some fishes occurred at higher temperatures than others. More accurate description of temperatures experienced by outfall-area fishes was permitted by measurements of their body temperatures.

Measurement of body temperatures confirmed partial segregation among species with respect to temperature. During afternoon, median body temperatures of carp, pumpkinseeds, bluegills, and largemouth bass were above 29 C, while those of yellow bass, rock bass, black crappies, and yellow perch were below 29 C. At night, only longnose gar and carp had median body temperatures above 29 C, while yellow bass, rock bass, pumpkinseeds, bluegills,

largemouth bass, and black crappies had median body temperatures below 29 C.

2. During late summer, young bluegills at different locations in the outfall area were similarly acclimated to temperatures within a narrow interval of the available spectrum.

Fish collected on five dates from four locations within the outfall area had estimated acclimation temperatures between 29.4 and 31.3 even though water temperatures varied between 25 and 36 C at the collection sites. To have attained acclimations between 29.4 and 31.3 C, young bluegills must have spent a majority of time at or below these temperatures and almost no time above 31.5 C.

This conclusion agreed substantially with the distribution of body temperatures observed for slightly larger young bluegills. The highest body temperature among 31 specimens was 31.8 C; the interquartile range of body temperatures was 28.8-31.2 C during afternoon and 27.0-29.0 C at night.

3. The more abundant a species was in the outfall area relative to reference areas during summer, the higher were the temperatures in the outfall area at which representatives of that species occurred.

During summer, median body temperatures of fishes in the outfall area were positively correlated with concentration of those fishes in outfall area relative to reference areas. The correlation was highly significant ($p < 0.01$) despite probable variation introduced by measuring body temperatures and abundances in different summers--body temperatures in 1970 and

abundances in 1968 and 1969.

Not only did fishes that were concentrated both day and night in the outfall area live there at higher temperatures than representatives of groups that were never concentrated in the outfall area (e.g., large carp vs. large rock bass), but also daily changes in the distribution of other fishes were accompanied by changes in the temperatures they occupied in the outfall area. Large yellow bass, medium and large bluegills, and largemouth bass were concentrated in the outfall area during afternoon but were more evenly distributed at night; within the outfall area, these fishes occurred at higher temperatures during afternoon than at night. There was little daily change in outfall-area temperatures occupied by large carp and large rock bass, whose distributions remained similar from day to night.

Only large pumpkinseeds during afternoon deviated markedly from the apparent relationship between body temperature and concentration in the outfall area. During afternoon, large pumpkinseeds occurred in water about 2.5 C warmer than was consistent with their position in the array of relative abundances. Many of these fish, including those with highest body temperatures, were caught in or near the discharge jets, to which they may have been attacked by factors other than temperature. At night, large pumpkinseeds did not aggregate near the outfalls and had a median body temperature of 28 C, the same as other fishes in similar relative abundance.

4. Diurnal temperature distributions of six species in the outfall area during August conformed to the distributions of temperature they maintained by behavioral thermoregulation in the laboratory.

Those fishes which regulated higher temperatures in the laboratory occurred at higher temperatures in the outfall area. Moreover, all species except yellow perch had median body temperatures in the outfall area within 1.2 C of the midpoint of the preferred range in the laboratory.

Yellow perch avoided the outfall area. The few individuals which did occur in the outfall area lived in water that was the coolest available but still warmer than the upper turn-around temperature, 26.5 C. There was little water anywhere in the littoral zone cooler than 26.5 C in August 1970.

Nocturnal temperature distributions of five species (only 2 yellow perch were caught at night) were correlated somewhat less well with thermoregulatory limits than were diurnal distributions. Some fishes in the outfall area, notably bluegills and largemouth bass, occurred at temperatures lower at night than during afternoon. While laboratory fish probably spent more time near the lower turn-around temperatures at night than during the day, turn-around temperatures remained the same from day to night and did not, therefore, reflect the downward shift in average temperatures the fish maintained.

Temperature distributions of fishes in the outfall area were assessed from specimens generally larger than those used in the thermoregulation experiment. Only the comparisons for

bluegills, largemouth bass during the day, and yellow perch could be based on fish of similar size. In the other cases, few or no field data were collected from specimens as small as those convenient for use in experiments.

Considering that field and laboratory data were reasonably consistent despite variation in the sizes of fish compared, the following conclusion was suggested: The different temperature distributions of six species within the outfall area resulted from species-specific behavioral thermoregulation.

Coutant (1970), in a review of both published and unpublished literature on reactions of fishes to heated discharges, did not cite empirical evidence that fish distributions in outfall areas correspond with their thermoregulatory performances in experimental temperature gradients.

In summary, major features of the littoral distributions of Monona fishes during summer were consistent with the following explanation: Temperature was a major factor governing fish distribution, in that fish tended to be most abundant in that part of the habitat having temperatures within or nearest a species-specific preferred range of temperature determined in the laboratory. Disparate distributions of some conspecific fish of different size resulted from the influence of factors other than size-related differences in preferred temperature.

Fish distributions and non-thermal factors--food, predators, currents

Temperature has been almost universally regarded as the primary factor governing the use of outfall areas by fishes (Alabaster, 1964, 1969; Alabaster and Downing, 1966; Allen,

Boydstun, and Garcia, 1970; Dryer and Benson, 1957; Gammon, 1971; Mihursky, 1967; Mount, 1969; de Sylva, 1969; Trembley, 1961). In general, distributions of Lake Monona fishes in conjunction with laboratory results supported the hypothesis of thermal primacy.

However, some aspects of the distributions of Monona fishes indicated the influence of factors other than temperature. Spatial segregation of young and adults of two species, carp and yellow bass, probably did not reflect size differences in preferred temperature. Adult carp were concentrated in the outfall area during summer, but young carp were not. Thermoregulatory behavior of young carp indicated that they preferred temperatures between 30 and 33.5 C--temperatures available only in the outfall area. Young yellow bass avoided the outfallarea, but larger fish were relatively abundant there and were particularly concentrated near the jets. Yet, large yellow bass stayed near the bottom in water not much warmer than the reference areas where the young lived. Young rock bass were concentrated in the outfall area but lived at essentially normal littoral temperatures by avoiding locations near and between the jets. Large pumpkinseeds, although not concentrated in the outfallarea as a whole, lived near the outfalls during afternoon at temperatures approaching the maximum effluent temperature. Finally, greater abundance of young black crappies in the outfall area during August 1968 but in the reference areas during July-August 1969 could not be attributed to a temperature difference between years.

Although solutions are not offered for all problems referenced

in the previous paragraph, some insight into their probable complexity is suggested by consideration of non-thermal aspects of the outfall environment. Non-thermal agents may have operated either independently or synergistically with each other and temperature to influence use of the outfall area by fishes

One non-thermal effect of the power plant's operation was to increase the abundance of zooplankton in the littoral zone. Samples[1] of zooplankton and young bluegills from the study areas during summer 1969 showed that

1. limnetic zooplankters, primarily Daphnia sp. and copepods, were four to ten times more abundant in the outfall area than in reference areas, where densities of 5 to 20 animals/liter normally occurred;

2. limnetic zooplankters were very concentrated near each outfall (densities up to 350 animals/liter) and sometimes eddied at the surface in floating "mats" several animals thick and as much as a few meters in diameter; and

3. young bluegills in reference areas fed primarily on the littoral amphipod, Hyalella azteca (87% of the items in sampled stomachs), but young bluegills in the outfall area ate primarily limnetic zooplankton (93% of the items in stomachs).

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[1]The work summarized here represents combined efforts of John J. Magnuson, Garrett Brauer and myself. More detailed accounts of the methods and results of this research are presented in a partial technical completion report entitled, "The Effect of a Power Plant on the Distribution and Abundance of Zooplankton Near the Plants' Thermal Outfall". This report is available from the Office of Water Resources Research under the project number B-028-WIS.

Thus, the supply of food for fish in part of the normally zooplankton-poor littoral zone was enriched by the discharge of water containing limnetic zooplankton (after circulation through the power plant's cooling system). Young bluegills and probably other planktivorous fishes were able to exploit this food resource.

The concentration of displaced zooplankton in the outfall area may have attracted such fishes as yellow bass, pumpkinseeds, bluegills, and young largemouth bass. Fishes are known to aggregate in areas where planktonic food is relatively abundant (McNaught and Hasler, 1961; Schaefer, 1961; Lucas, 1956).

Laboratory experiments with bluegills and yellow perch confirmed that fishes may be attracted to food-rich environments, but suggested that attraction to food does not override behavioral thermoregulation. Provided an environment with the preferred temperature is available, the fraction of time spent in a food-rich environment is likely to decrease abruptly as its temperature diverges from the preferred. Fishes may, however, briefly foray from an environment offering the preferred temperature but not food into cooler or warmer (even lethally warm) water where food is available.

Although planktonic food for fish was relatively concentrated in the outfallarea, so too was at least one of the major fish predators of Lake Monona--the longnose gar. During summer 1968, gar in the outfall area fed primarily on young bluegills (Haase, 1969), which were very abundant. Low densities in the outfall area of young carp and young black bullheads may have resulted in part from predation by gar. Evidence from Lake

Mendota suggests that young carp are more vulnerable to gar than are young bluegills and other spiny-rayed fishes (Haase, 1969).

The flow of water from the outfalls may have influenced the formation and maintenance of fish aggregations at the primary outfall during late winter and spring. Adult yellow bass, which dominated outfall aggregations, also concentrated during the same season in the swiftly flowing water below a navigation lock on the Yahara River between Lakes Mendota and Monona. The temperature of the river was about 8 C, while the heated effluent was 14-20 C.

To close the discussion of non-thermal effects, we note that low concentrations of dissolved oxygen were not observed in the outfall area. Water in the outfall area during summer 1968 was supersaturated (up to 115%) with oxygen.

Responses of Lake Monona fishes to power plant operation: Present assessment and some unresolved problems

Investigation of the distributional ecology of fishes in Lake Monona's littoral zone, laboratory experiments on behavioral thermoregulation of fishes, and information from the literature suggested the following major conclusions:

1. Distributions of fishes within the littoral zone of Lake Monona were markedly and differentially influenced by the discharge of heated effluent.
2. Major features of the distributions during summer resulted from fishes' different responses to elevated temperatures of the outfall area.

3. During summer, fishes concentrated in the outfall area and, within it, distributed themselves primarily in accordance with thermoregulatory behavior, whereby each individual tended to maximize its exposure to temperatures within the preferred range of the species.
4. Behavioral thermoregulation was not overridden, but in some cases may have been modified, by behavioral responses to the outfall area's peculiar non-thermal features--abundant food, strong currents, concentrated predators.

Our work did not provide empirical evidence that Monona fishes responded to operation of the power plant with ecological prudence--i.e., that fishes concentrated in that fraction of the habitat which was optimum for performance of their life processes. An attempt to assess one measure of young fishes' ecological success--growth rate--yielded results confounded by size-differential movements of the fish. Thus, information from other studies must constitute the basis for conjecture as to whether distributions of Monona fishes reflected preference for optimum habitats.

It seems logical that fishes ought to prefer environments which are, in some sense, optimum. Experimental evidence from the literature confirms that preferred and optimum temperatures of fishes are highly correlated when other components of environment are not limiting. The mid-point of young bluegills' preferred temperature range is 30 C; this is also the temperature at which bluegills grow most rapidly (Maloney, 1949).

However, the optimum temperature for growth and perhaps other activities varies with the availability of food, whereas the final temperature preferendum may not. When Brett, Shelbourn, and Shoop (1969) provided young sockeye salmon (Oncorhynchus nerka) with excess food, growth was most rapid at temperatures near the final preferendum, 14 C. But when food was restricted to 1.5% of dry body weight per day, the optimum temperature for growth decreased to 5 C.

If, when food is limiting, the optimum temperature for growth decreases and the correspondence between optimum and preferred temperatures is to be maintained, the final temperature preferendum must also decrease. Indirect evidence suggests, to the contrary, that the final temperature preferendum may not be greatly influenced for food supply. The relationship between preferred temperature and feeding level has not been systematically evaluated, but temperatures preferred by starved fishes have been reported. Atlantic salmon (Salmo salar), brook trout (Salvelinus fontinalis), and rainbow trout--all starved two or three weeks--preferred respective temperatures 2 C higher, 2 C lower, and 4 C lower than did fed controls (Javaid and Anderson, 1967). These data suggest that starved fishes prefer temperatures only slightly lower or even higher than those preferred by well-fed fish.

Both planktivorous and piscivorous fishes of Lake Monona had access to abundant food in the outfall area. Thus, fishes which during summer lived at preferred temperatures in the

outfall area also encountered conditions that were presumably optimum for growth.

But if food had been deficient in the outfall area, we believe that distributional responses of fishes would have been little different from those observed. Both temperature preferences of starved fishes (Javaid and Anderson, 1967) and the behavior of bluegills and yellow perch offered food at extreme temperatures suggest that fishes tend to prefer certain species-specific temperatures regardless of whether or not food is available at those temperatures. Thus, a food-deficient outfall area might be expected to attract fishes which prefer high temperatures even though it would offer poorer conditions for their maintenance and growth than would be available in unheated parts of the habitat.

Whether significant advantages or disadvantages accrue to individual fish in outfall areas depends not only on "quality" of the outfall environment but also on the amount of time the fish lives there.

Although fish distributions in Lake Monona were treated as if static, dynamic features were recognized. The study areas certainly did not consist of closed systems, each with its own resident populations of fish. Rather, at any instant the assemblage of fishes in a part of the littoral zone consisted of individuals which had been there for different periods of time. That a very small fraction of marked fishes was recaptured suggested that larger fish resided in the study areas no longer

than several days before they were replaced by new immigrants. Many larger fishes (adult bluegills, yellow bass) must have stayed in the littoral zone no more than 12 hrs consecutively, because the individuals present in the study areas were obviously fewer during the day than at night. Presumably, smaller fishes moved about less than larger ones. However, daily changes in length-frequency distributions suggested that even small bluegills made onshore-offshore movements.

Further evaluation of the power plants' impact on fishes must await answers to the following questions pertaining to dynamic aspects of fish distribution:

1. How do fishes arrive in the outfall area?
2. How long do individual fish stay in the outfall area?
3. What factors cause fish to leave the outfall area?
4. Once a given fish has left the outfall area, is it likely to return and, if so, how soon?

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